The tympanal organ of *Acridomorpha*

(Orthoptera)

BY

JOYCE B. MASON.

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INTRODUCTION.

It has long been known that the tympanal organ varies greatly in external structure in the suborder *Acridomorpha* (Knetsch, 1939), but no comprehensive study of it in all families and subfamilies has hitherto been made.

This paper present the results of a study of the external morphology of the tympanal organ in relation to taxonomy, wing development and sound-producing mechanisms in all families and subfamilies of *Acridomorpha*.

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SYPNOPSIS.

The tympanal organ of the majority (915) of genera of *Acridomorpha* has been studied from the point of view of gross external morphology.

It was found that the morphology of the tympanal organ has a certain taxonomic value for most superfamilies, families, and subfamilies, and sometimes for genera.

The size of the membrane is negatively correlated with tegmina length, except in apterous species, but the size of the dorsal shell covering and that of the subtympanal lobe are positively correlated with tegmina length.

Sexual dimorphism is found in the general morphological structure of the organ in a few species. It is particularly characteristic in the subfamily *Porthetinae* where the males have transparent membranes and are macropterous, while the females have sclerotised membranes and are apterous.

Statistical analysis shows that the males have relatively much larger membranes than the females, in every family or subfamily of *Acrodomorpha.*

Truxalinae and *Eremogryllinae* possess relatively larger membranes than the other subfamilies; *Cyrtacanthacridinae* the smallest. *Pamphagidae, Pyrgomorphidae* and *Romaleinae* also have relatively small membranes.

Highly developed sound-producing mechanisms may be present when the tympanal organ is absent, the tympanal organ may be present when there is no apparent sound-producing mechanism, or both may be present. Species with small or very large membranes may possess well developed sound-producing mechanisms. It appears that a well developed sound-producing mechanism, the presence of a tympanal organ and a large membrane do not necessarily coincide.

Material and methods.

The material studied was that of the collection of the British Museum (Natural History), of which 915 genera were examined. Both sexes were used when they were available in the same species, and one species was studied in each genus. The numbers of genera and of males and females studied in each family or subfamily that was treated as an entity are shown in Table 1; the number of specimens studied is given in each table (Tables 1-13), the total under each heading being shown without regard to species.

The external structure of the tympanal organ was examined, sketches and notes being made of any outstanding features. The results were grouped according to the morphological features, and the groups were then compared with the conventional systematic groups. The presence or absence of sound-producing mechanisms and relevant measurements were also recorded. All notes and data on individual species are preserved in the library of the Anti-Locust Research Centre.

The largest diameter of the tympanal membrane was measured with

callipers in mm to the first decimal figure. This was found to be the most convenient method owing to variation in the inclination of the membrane in relation to be body surface. The largest diameter was always from the lower posterior corner to the upper anterior corner of the membrane.

All other measurements were also made with callipers in mm to the first decimal point, always on the left side of the body in the case of paired structures. The maximum body length (L) was measured from the end of the fastigium of the vertex of the head to the end of the abdomen, care being taken to choose specimens not distorted. In the meso — and meta-thoracic region, i. e. between the hind femur and the middle leg, the body width (W) was measured, being maximal at this point in all species.

As neither the volume nor the area of the insect could be exactly calculated, the measurements for length and width were multiplied (L × W). This gave a figure, the body size index, indicating a relative body size. An index for the tympanum was then calculated by dividing the diameter of the tympanal membrane (D) by the body size index; as this gave a figure of five or six decimal places, the product was multiplied by 1000. For example, in *Schistocerca gregaria,* the female body length (L) was 55.0 mm, the width (W) 10.4 mm, the diameter of the tympanal membrane (D) 3.0 mm; (L × W) 572.0; D/LW = 0.00524; and the Tympanal Index 5.24.

Terminology and explanation of symbols.

In previous works on the tympanal organ, a most complicated nomenclature is found for its various structures. In order to clarify the confusion a list of terms and abbreviations used in this paper (put in alphabetical order of the abbreviations) is given below, together with definitions of the terms and with the main synonyms used by the following authors: Berlese 1909, Beier 1934, Chopard 1955, Eggers 1928, Graber 1876, Hers 1938, Imms 1957, Jannone 1939, Knetsch 1939, Müller 1826, Schwabe 1906, Snodgrass 1935, Weber 1933.

Bulbous body. A large bulbous region of the sensory structure of the tympanal organ found only in *Pamphagidae.* This region is a large sclerotized part of the sensory structure which protrudes above the level of the outer surface of the membrane.

Dhp — depression of horny process for tensor muscle (fig. 1).

A small depression beneath the spiracle, indicating the position of an internal horny process to which a tensor muscle is attached. *(Zungen- oder stachelförmige Chitinsehne d. Spannmuskels* Graber, 1876; *Öff-*

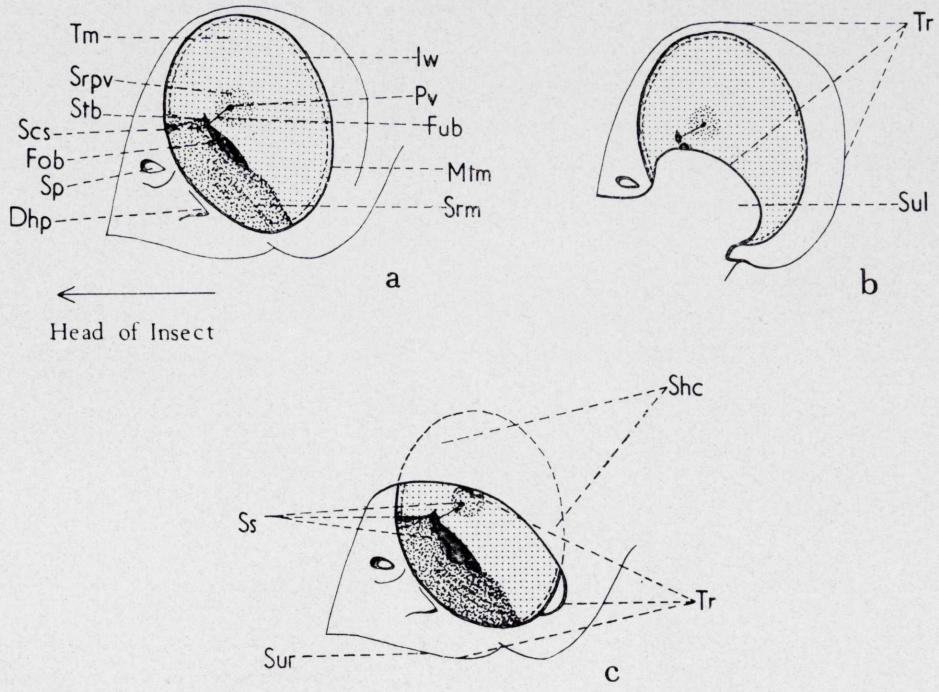


Fig. 1.—Terminology: *a)* structures on the tympanal membrane; *b)* the tympanal membrane and development of a moderate-sized subtympanal lobe; *c)* the tympanal membrane and development of a dorsal shell covering.

nung des Stigmenfeldzapfens Schwabe, 1906, Eggers, 1928, Beier, 1934; *Processo del campo stigmatico* Berlese, 1909; *Stigmenfeld* Weber, 1933; *Campo stigmatico timpanale* Jannone, 1939.)

Fob — folded body (fig. 1).

An elongate sclerotization on the tympanal membrane; the largest of the supporting projections of the sensory structure in *Acrididae* and *Ommexechidae. (Rinnenförmige Trommelfellverdickung (Körperchen),* Graber, 1876; *Rinnenförmiges Körperchen* Schwabe, 1906; Eggers, 1928; Beier, 1934; Knetsch, 1939; *Horny process* Imms, 1957; *Arm supporting sense organ* Snodgrass, 1935; *La rainure et la crête*

Hers, 1938; *Sclerite principale o inferior di sostengo dello stesso* Jannone, 1939; *Corps en forme de gouttière* Chopard, 1955).

Fub — fusiform body (fig. 1).

An internal structure, but it can be seen externally through the thin tympanal membrane. It is a part of the sensory structure and consists of a thin tissue passing from the pyriform vesicle to the internal Müller's organ. Therefore externally the fusiform body appears as a thin line joining the pyriform vesicle and the folded body. It is present in the families *Acrididae, Pauliniidae* and *Ommexechidae. (Processo fusiforme* Berlese, 1909; *Spindelförmiger Fortsatz des nervösen Endorgans* Eggers, 1928; Beier, 1934; *Corpuscolo fusiforme* Jannone, 1939.)

Iw — internal white margin (fig. 1).

A pale narrow margin running parallel to the upper and posterior margin of the membrane. It is an internal supporting structure which can often be seen through the thin membrane.

Müller's organ.

The most prominent part of the sensory region of the tympanal organ, situated internally under the membrane and below the external sclerotic supports. It consists of a swelling of nervous tissue and forms the termination of the nerve. *(Müller'sches oder Tympanalganglion* Graber, 1876; *Organo apicale* Berlese, 1909; *Müller's organ* Imms, 1957; *Scolopophorous sense organ* Snodgrass, 1935; *Organe nerveux tympanal* Hers, 1938; *Organo apicale di Müller* Jannone, 1939; *Tympanales Endorgan* Eggers, 1928; Beier, 1934; *Organe terminal* Chopard, 1955.)

Mtm — margin of the tympanal membrane (fig. 1).

The outer limit of the tympanal membrane, where the membrane is connected to the body wall.

Pv — pyriform vesicle (fig. 1).

A small pear-shaped vesicle situated posteriorly to the sclerotic supports of the sensory structure. This is connected to the spindle-shaped fusiform body. *(Birnförmiges Körperchen* Graber, 1876; Schwabe, 1906; Eggers, 1928; Beier, 1934; Knetsch, 1939; *Corpuscolo piriforme* Berlese, 1909; *Pyriform vesicle* Imms, 1957; *Pyriform sclerite* Snod-

grass, 1935; *Poire* Hers, 1938; *Sclerite piriforme* Jannone, 1939; *Corps piriforme* Chopard, 1955.)

Supporting body.

An external supporting sclerotic structure. There is only one such sclerite on the membrane of *Pyrgomorphidae* and *Pamphagidae,* whereas in *Pauliniidae* there are three, a large sclerotized body, a fusiform body and a pyriform vesicle. The term supporting body is given to the largest sclerotized body. This body may represent a fusion of the styliform body and the folded body or only the folded body.

Scs — sclerotic cavity of the sensory structure (fig. 1).

A small cavity at the apex of the folded body and the styliform body. Externally it appears roughly circular, but in fact it is a cone-shaped chitinous depression which passes into the internal Müller's organ. *(Öffnung des zapfenförmigen Körperchens* Graber, 1876; Schwabe, 1906; Eggers, 1928; *Aperture del corpuscolo a corno* Berlese, 1909; *Cone* Hers, 1938; *Zapfen* Knetsch, 1939; *Apertura dell'infundibulo a fondo cieco scavato nello stello* Jannone, 1939.)

Sensory structure.

A general term used for the sclerotic structures as seen through the outer surface of the membrane, i. e. folded body, styliform body, pyriform vesicle and the nerve-like fusiform body.

Shc — shell-like covering (fig. 1).

The extension of the dorsal side of the tympanal rim which overhangs the membrane as a shell-like structure. *(Obere Trommelfelleiste* Graber, 1876; *Obere Tympanaleinfassung* Schwabe, 1906; Eggers, 1928; *Hintere Tympanalleiste* Weber, 1933; *Tympanal capsule* Snodgrass, 1935; *Le capuchon* Hers, 1938; *Capsule tympanica* Jannone, 1939.)

Sp — first abdominal spiracle (fig. 1).

The spiracle which is situated in front of and close to the tympanal organ.

Srm — sclerotized region of the membrane (fig. 1).

The region between the sclerotized supports of the sensory structure and the lower margin of the membrane.

Srpv — sclerotized region surrounding the pyriform vesicle (fig. 1).

This is a sclerotization of the membrane surrounding the pyriform vesicle and the fusiform body.

Ss — Sclerotic supports (fig. 1).

A general term used for the complex of external sclerotized structures (folded body, styliform body, supporting body, pyriform vesicle) on the tympanal membrane supporting the internal sense organ. (*Trommelfell Körperchen* Weber, 1933; *Tympanal sense organ and its supports* Snodgrass, 1935; *Tronmelfellkörper* Knetsch, 1939.)

Stb — styliform body (fig. 1).

The upper anterior sclerotic support of the sensory structure. It is much smaller than the folded body, and larger than the pyriform vesicle, and is often surrounded by a more sclerotized region of the membrane (Srm.). (*Basalplatte des stielförmigen Körperchens* Graber, 1876; Schwabe, 1906; Eggers, 1928; Beier, 1934; *Piastra basale del corpuscolo stiliforme* Berlese, 1909; *Horny process* Imms, 1957; *Arm supporting sense organ* Snodgrass, 1935; *Manche* Hers, 1938; *Stielförmiges Körperchen* Knetsch, 1939; *Sclerite superiore di sostegno del precedente* Jannone, 1939; *Corps en forme de poinçon* Chopard, 1955.)

Sul — subtympanal lobe (fig. 1).

The extension of the lower tympanal rim which is itself an extension of the metathorax. The subtympanal lobe covers the anterior region of the membrane. In extreme forms, the lobe completely covers the sclerotic supports on the tympanal membrane. In other forms the lobe does not overlap the membrane but lies slightly below its margin. (*Untere Tympanalleiste* Graber, 1876; Schwabe, 1906; Knetsch, 1939; *Vordere Tympanalleiste* Weber, 1933; *Subtympanal lobe of the metathorax* Snodgrass, 1935; *Lobo subtimpanico del metaepimero* Jannone, 1939.)

Sur —Subtympanal ridge (fig. 1).

A very reduced subtympanal lobe, in the form of a ridge. The subtympanal ridge is a continuity of the tympanal rim, extending from just beneath the spiracle to the lower posterior margin of the membrane. (*Bord inférieur* Hers, 1938; *Untere Tympanalleiste* Graber, 1876; Beier, 1955; *Untere Tympanaleinfassung* Eggers, 1928.)

Tm — tympanal membrane (fig. 1).

A transparent membrane stretched across the tympanal opening. Sometimes the membrane is partly or completely sclerotized. (*Trommelfell* Müller, 1826; *Hinteres, glattes Tympanalfeld* Graber, 1876; *Hinteres Tympanalfeld* Eggers, 1928; *Tympanum* Imms, 1957; Weber, 1933; Snodgrass, 1935; *Tympanalfeld* Schwabe, 1906; Beier, 1934; *Tympano* Berlese, 1909; Jannone, 1939; *Membrane tympanale* Hers, 1938; Chopard, 1955.)

Tympanal organ.

This is the general term for the organ as a whole, situated on either side the first abdominal tergite. (*Tympanal Organe* Schwabe, 1906; Weber, 1933; Knetsch, 1939; *Campo del timpano* Berlese, 1909; *Tympanal organ* Imms, 1957; Snodgrass, 1935; *Organe tympanal* Hers, 1938; *Organo dell'udito* Jannone, 1939; *L'organe auditif* Chopard, 1955; *Trommelfell* Beier, 1934.)

Tr — tympanal rim (fig. 1).

The outher chitinous frame surrounding the tympanal organ. The development of it varies greatly. Dorsally, it originates from the first abdominal tergite and it may form a dorsal shell-like covering overlapping the membrane. Ventrally it may form a subtympanal lobe or ridge which originates from the metathorax. (*Hintere Trommelfelleinfassung* Schwabe, 1906 (partly); *Cornice timpanale* Berlese, 1909; *Tympanum with its border* Imms, 1957; *Cadre chitineux* Hers, 1938; Chopard, 1955; *Innere Tympanalleiste* Knetsch, 1939; *Cornice timpanica* Jannone, 1939; *Tympanalleiste* Beier, 1934.)

External structure of the tympanal organ.
(Figs. 1, 2).

The tympanal organ situated on either side of the first abdominal tergite consists of a disc-shaped membrane with a sensory structure in its anterior region.

Surrounding the tympanal organ is a chitinous rim (tympanal rim) which may become specialised. Sometimes, when the membrane lies below the level of the body wall, the dorsal rim originating from the

first abdominal tergite may give rise to a shell-like covering which overlaps the dorsal region of the membrane.

Ventrally the tympanal rim may develop a large sub-tympanal lobe which originates from the metathoracic tergite and conceals the supporting sclerites of the sensory structure, but it may be reduced to a smaller lobe concealing only a small area of the membrane. In many cases the lobe is further reduced to only a small fold (sub-tympanal ridge), or it may be absent altogether.

Lying anterior to the membrane is the first abdominal spiracle. Also near the lower anterior margin of the membrane is a small depression which marks the position of an internal sclerotised process for the attachment of the tensor muscle.

The thin membrane is stretched across the tympanal opening. It is roughly oval or circular. When it is oval its long axis is inclined towards the head of the insect. The membrane is usually transparent, but it may be completely or partly opaque through sclerotisation. According to Gray (1960), who studied the fine structure with an electron microscope, the membrane of *Locusta migratoria migratorioides* R. & F. is 2-3 μ thick but increases to four times this thickness where the ganglion (Müller's organ) is attached. The external surface of the membrane is covered by spines 1-2 μ long.

The majority of tympanal organs have the membrane tilted at an angle in relation to the body surface, the upper and posterior margin being depressed into the abdomen, while the lower and anterior margin is level with the surface. In extreme cases the membrane is tilted as much as 75°-80° into the abdomen, so that it is almost at right-angles to the tergite. The upper margin of the membrane is usually more depressed than the lower margin. However, in some genera of *Pyrgomorphidae* the lower margin is also deeply depressed. The membrane may lie completely level with the body surface and is then often sclerotized.

TABLE 1.

Numbers of genera (males and females) studied in the families and subfamilies of Acridomorpha.

Name	Genera	♂	♀	Name	Genera	♂	♀
Eumastacoidea:				*Pauliniidae*	1	1	1
Eumastacidae.	37	24	32	*Acrididae*			
Proscopiidae.	11	9	9	*Dericorythinae*	4	4	4
Trigonopterygoidea:				*Chilacridinae*	5	2	5
Trigonopterygidae.	2	2	2	*Romaleinae*	37	28	33
Pneumoroidea:				*Lithidiinae*	3	1	3
Pneumoridae.	5	5	3	*Hemiacridinae*	43	31	35
Tanaoceridae.	2	2	1	*Tropidopolinae*	14	12	13
Xyronotidae.	1	1	1	*Oxyinae*	17	16	12
Acridoidea:				*Coptacridinae*	13	13	13
Charilaidae	2	2	2	*Calliptaminae*	11	11	11
Pamphagidae				*Euryphyminae*	14	13	14
Echinotropinae	3	1	3	*Eyprepocnemidinae*	27	22	23
Porthetinae	13	12	11	*Catantopinae*	245	182	221
Akicerinae	25	20	24	*Cyrtacanthacridinae*	24	22	24
Pamphaginae	25	18	23	*Egnatiinae*	5	5	5
Ommexechidae	4	4	4	*Acridinae*	150	147	148
Pyrgomorphidae	66	55	57	*Eremogryllinae*	2	2	2
Lentulidae	15	14	15	*Truxalinae*	85	85	84
Lathiceridae	4	3	3				

Near its outer margin and parallel to it the membrane has a white edge. This is an internal sclerotized supporting structure which shows through the membrane.

On the inner side of the membrane and situated anteriorly to its middle point lies the sensory structure which has a number of small sclerotic bodies which are considered to support the internal Müller's organ. Sometimes there are nerves beneath the membrane extending from the sclerotic bodies to the anterior ventral margin. However, because these are internal and are frequently covered by a more sclerotized region, no detailed study of them was undertaken in the present work.

Surrounding the sclerotic supports and extending to the lower anterior margin of the membrane there is a more sclerotized region of it. In some species it is difficult to differentiate the exact lower margin of

the membrane as the sclerotic region becomes gradually fused with the body wall.

The sclerotic supports of the sensory structure differ in number and form in the various families. As seen externally there may be one, two

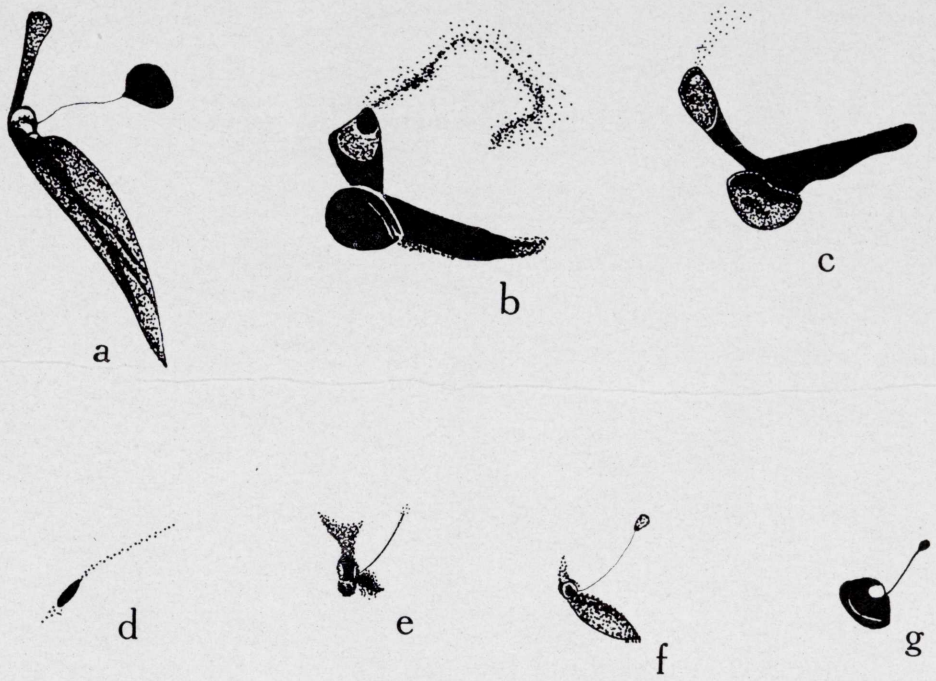


Fig. 2.—External sclerites of a sense organ: *a) Acrididae: Duronia chloronata; b) Pamphagidae: Tmethis cisti; c) Charilaidae: Charilaus carinatus; d) Pyrgomorphidae: Phyteumas olivaceus; e) Ommexechidae: Spathalium hispidum; f) Parossa bimaculata; g) Paulinidae: Paulinia acuminata.*

or three sclerotic bodies and nerve-like structures; details are given in the descriptions under families (fig. 2). They also tend to become reduced when the tympanal organ is itself poorly developed.

The tympanal organ in the various families.

All the families of *Acridomorpha* were studied in systematic order (Dirsh, 1966), with respect to the external structure of the tympanal organ, the presence or absence of it and of sound-producing mechanisms, and the degree of development of tegmina and wings.

Some families have no sound-producing mechanism and no tympanal organ. Some possess a stridulatory mechanism but no tympanal organ, some a tympanal organ but apparently no stridulatory mechanism, and some possess both. Below, all the families are reviewed from this point of view.

ACRIDOMORPHA

EUMASTACOIDEA.

EUMASTACIDAE.

The genera of *Eumastacidae* possess neither tympanal organ nor sound-producing mechanism in either sex, regardless of the presence or absence of wings.

PROSCOPIIDAE.

The representatives of this family studied have neither tympanal organ nor any known sound-producing mechanism. However, from living specimens high-pitched squeaks can be heard, but how the noise is produced is unknown. Most genera are apterous, but a few are micropterous.

TRIGONOPTERYGOIDEA.

TRIGONOPTERYGIDAE.

In the two genera of this family studied, neither tympanal organ nor sound-producing mechanism was detected. Both sexes are macropterous.

PNEUMOROIDEA.

PNEUMORIDAE.

The genera of this family all possess a well developed sound-producing mechanism of a special type. There is no tympanal organ. In the specimens studied the males are macropterous and females brachypterous or apterous.

TANAOCERIDAE.

In the only two genera of this family *(Tanaocerus* and *Mohavacris)* the tympanal organ is absent in both sexes. A well developed sound-producing mechanism is present in the males (Dirsh, 1955), but not in the female. Both sexes are apterous.

XYRONOTIDAE.

The tympanal organ is absent in both sexes of the only known genus. A sound-producing mechanism is present in the male only. Both sexes are apterous.

ACRIDOIDEA.

CHARILAIDAE.

(Fig. 2, *c*).

Two genera, *Charilaus* and *Hemicharilaus,* of this family were studied. Both have tympanal organs similar to those in *Pamphagidae.* The membrane is oval and slightly depressed posteriorly. Both have only indications of a subtympanal lobe. The sclerotic supports of the sensory structure are similar to those of *Pamphagidae* (fig. 2, *b*) there is a supporting bulbous body with two finger-like projections which are level with the membrane. One projection points towards the antero-dorsal margin of the membrane, at the apex of which is small cavity or circular depression; the other points towards the postero-dorsal margin. A more sclerotized region curves backwards from the small sclerotic cavity.

A sound-producing mechanism is apparent in the genus *Charilaus,* but not detectable in *Hemicharilaus.*

PAMPHAGIDAE.

(Fig. 3, Table 2).

With the exception of a few genera this family possesses a tympanal organ. The membrane is approximately oval, usually transparent and

posteriorly slightly depressed beneath the body wall. The greatest diameter of the membrane usually slopes only slightly towards the head of the insect but in some cases it is more inclined. The tympanal rim sometimes slightly overlaps the membrane dorsally, but there is no large shell-like covering in this family. All species possess a subtympanal lobe or ridge, except those in which the tympanal organ is very poorly developed. This is an interesting feature, as in *Acrididae* a large subtympanal lobe always accompanies a large dorsal shell covering. The sclerotic supports of the sensory structure consist of a single bulbous body raised above the tympanal membrane, and two finger-like projections arising from it, one pointing towards the antero-dorsal region of the membrane, at the apex of which there is usually a small sclerotic cavity, and the other pointing posteriorly. The projections are less raised above the membrane than the bulbous body. In some species the projections are very reduced, particularly the posterior one. The bulbous body is more pronounced in some genera than in others; it may be completely surrounded by a more sclerotized area of the membrane but very often the sclerotized region passes from the supporting body to the subtympanal lobe or ridge. A sclerotized region also completely surrounds the anterior projection and continues upwards in a curve bending backwards over the supporting body; the centre line of the curve is more sclerotized than the edges, and the curve varies in length, and may be reduced when the projection is smaller. The tympanal membrane is sometimes completely sclerotized.

The genera of *Pamphagidae* may be divided into four groups according to the features of the tympanal organ as described below; a more detailed account is given in the descriptions of the subfamilies, as each subfamily exhibits different morphological trends. As in other families, the morphology of the tympanal organ varies with the length of the tegmina (Table 2). The first group has a large subtympanal lobe completely or partly covering the sensory structure (fig. 3 *a, b*). The second group possesses a smaller subtympanal lobe not covering the sense organ (fig. 3, *c*). The third group is distinguished by a subtympanal ridge only and lobe (fig. 3, *d*); the membrane may be transparent or sclerotized. The fourth group has no tympanal organ; the species are apterous or, rarely, micropterous.

A sound-producing mechanism may be well or poorly developed, according to the tegmen size, or may be absent. However, there are sometimes specialised mechanisms which are not correlated with the

tegmina. When sound-producing mechanisms are studied in dried specimens only, as in the present case, they can only be recorded when the structures concerned are specialised and obvious.

Of the four subfamilies, *Akicerinae* have the most complex structure of the tympanal organ, with a well developed subtympanal lobe.

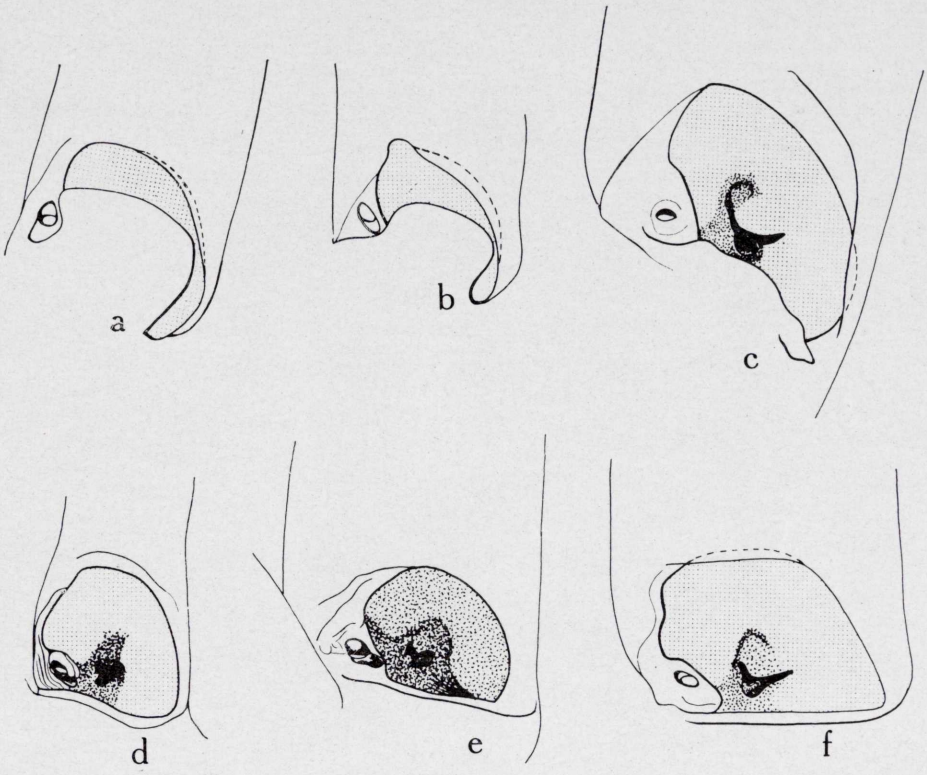


Fig. 3.—*Pamphagidae: Akicerinae: a) Tmethis cisti,* 2.5 mm.; *b) Eremocharis granulosa brachycera,* 3.0 mm. *e) Adephagus cristatus,* 2,6 mm.; *Porthetinae; d) Lobosceliana femoralis,* ♂ 3.3 mm.; *e) L. femoralis,* ♀ 3.8 mm.; *f) Pamphaginae: Acinipe crassicornis,* 2.2 mm.

Porthetinae show specialisation with extreme sexual dimorphism. *Pamphaginae* are less complex with no subtympanal lobe, and the membrane is sometimes sclerotized or the tympanal organ may be absent. The very small subfamily *Echinotropinae* has mixed characters, but with a tendency for simplification and reduction of characters.

ECHINOTROPINAE.
(Table 2).

There are only three genera in this small subfamily. Only four specimens were studied.

Geloiomimus spinosus Dirsh, 1955 shows sexual dimorphism. The male possesses a small tympanal organ, with a transparent membrane and small subtympanal lobe. The female has only a small sclerotized membrane, so illdefined that no measurements were made.

Only one female of *Echinotropis horrida* Saussure, 1899 was available for study, and this also has a poorly developed, sclerotized tympanal organ.

Only one female of *Thrincotropis capensis* Miller, 1932 was studied. This is a very remarkable species, as although the tegmina are micropterous, the tympanal organ is absent. This condition is rarely found in *Pamphagidae.*

In all females of this subfamily the tegmina are micropterous, and the tympanal organ if present is sclerotized and poorly developed. The male of *Geloiomimus spinosus* is macropterous and the tympanal membrane transparent. In general, the tympanal organ seems to be poorly developed. Sound-producing mechanisms are unknown.

PORTHETINAE.
(Fig. 3, *d, e;* Table 2).

The majority of genera show extreme sexual dimorphism of the tympanal organ, and has macropterous males and apterous females.

The whole subfamily possesses a tympanal organ of the type referred to above as the third group, i. e. with a subtympanal ridge and no lobe. All the males have a transparent membrane which is slightly depressed posteriorly. The sensory structure is of the usual *Pamphagidae* type, but the sclerotic supports are reduced, particularly the posterior projection. The bulbous part of the supporting body is more pronounced. The females have a tympanal membrane which is sclerotized, and is not depressed as in the males. The sensory structure, although very bulbous, is reduced, often with the posterior projections absent. The sclerotized membrane is never covered by the tegmen.

TABLE 2.

Family PAMPHAGIDAE.

Variation of the tympanal organ in relation to tegmen length and presence or absence of a sound-producing mechanism (+ present, — absent).

Subfamily	Tympanal organ					Wing Development (Number of specimens studied)								Sound-producing mechanism
						Macropterous		Brachypterous		Micropterous		Apterous		
	Membrane	Shell cover	Large lobe	Small lobe	Ridge	♂	♀	♂	♀	♂	♀	♂	♀	
Echinotropinae	Transparent, well developed.	—	—	+	—	1								None detected in the four specimens studied.
	Sclerotized, poorly developed.	—	—	—	—						2			
	Absent.	—	—	—	—						1			
Porthetinae	Transparent, well developed.	—	—	—	+	9				3	1			Present.
	Sclerotized.	—	—	—	+								10	None detected.
Akicerinae	Transparent, well developed.	—	+	—	—	9	8		2					+
	"	—	—	+	—	7	5	2	1	1	7			+
	"	—	—	—	+					1	1			+
Pamphaginae	Transparent, well developed.	Reduced or absent.	—	—	+					12	13			None detected.
	Slightly sclerotized.	Reduced or absent.	—	—	+					3	4			"
	Absent.	Absent.	—	—	—						2	3	4	"

These striking features, with the male and female having almost opposite characters, are very unusual. Also the association of the absence of the subtympanal lobe with well developed macropterous tegmina in the males is unusual in this family. These characters suggest a degree of specialisation within the family.

In the following species, all of which were studied, the males are macropterous and the females apterous: *Hoplolopha horrida* (Burmeister, 1938), *Lamarckiana cucullata* (Stoll, 1813), *Lobosceliana loboscelis* (Schaum, 1853), *Porthetis carinata* (Linnaeus, 1758), *Stolliana angusticornis* Dirsh, 1958, *Xiphoceriana brunneriana* (Saussure, 1887). One apterous female of *Pagopedilum brevis* (Walker, 1870), and one macropterous male, of *Puncticornia puncticornis* (Stål, 1876), were studied. In the species *Cultrinotus distanti* Saussure, 1892 and *Transvaaliana distanti* (Saussure, 1892) the males are micropterous and the females apterous, while in the species *Vansoniacris rubricornis* Dirsh, 1956, the male is brachypterous and the female apterous.

Trachypetrella andessonii (Stål, 1875) is the only species studied that is not dimorphic. Both sexes have a transparent membrane slightly depressed beneath the body wall. There is no subtympanal lobe. The sensory structure is reduced slightly and the posterior projection is absent. Both sexes are micropterous.

One male specimen of *Aphantotropis connectens* Uvarov, 1924 was examined. The membrane is transparent and similar to the others of the group. Unfortunately there is no female available to show if this species is dimorphic or not. The male is macropterous.

A sound-producing mechanism of a special kind is one of the main characters of the subfamily (Dirsh, 1961). The males possess stridulatory veinlets in the costal area of the tegmina. In *Trachypetrella* two kinds of sound-producing mechanism are very pronounced; in *Trachypetrella anderssonii* the tympanal membrane is very small.

Akicerinae.

(Fig. 3, *a, b, c;* Table 2).

All the species examined possess a tympanal organ. The membrane is transparent and slightly depressed. Sometimes it has a small projection at the antero-dorsal margin. There is a slight tendency for the dorsal rim to form a very small shell covering, but this is never deve-

loped to a great extent as it is in *Acrididae*. All species except *Hoplotropis brunneriana* Saussure, 1888 possess a subtympanal lobe. All the other species may be divided into two groups according to the size of the lobe.

In the first group a large subtympanal lobe (fig. 3, *a*) covers the sensory structure completely as in *Utubius* or partly as in *Thrinchus*. The sclerotic supports generally have larger projections than those in other *Pamphagidae*. Males and females are similar. The genera are macropterous or brachypterous.

The following species belonging to the large-lobe group were examined: *Eremocharis granulosa* (Walker, 1872), *Eremopeza gibbera angusta* (Uvarov, 1934), *Eremotmethis carinatus* (Fabricius, 1775), *Iranotmethis zagrosi* Uvarov, 1933, *Melanotmethis fuscipennis* (Redtenbacher, 1889), *Strumiger desertorum* Zubovskij, 1896, *Thrinchus variegatus* Tarbinsky, 1926, *Tmethis cisti clavelii* (Lucas, 1851), *Tuarega insignis* (Lucas, 1851), *Utubis syriacus zaharae* (Uvarov, 1940).

The second group can be distinguished by the smaller subtympanal lobe, which does not cover the sclerotic supports of the sensory structure. As in the large-lobe group, the membrane is depressed and in some species there is a slight projection at the anterior margin. The sclerotic supports have reduced projections and the bulbous part is frequently more prominent than in the large-lobe group. The genera are macropterous, brachypterous or micropterous, but not apterous. *Atrichotmethis semenovi* (Zubovskij, 1899) has the largest lobe found in this group; male and female are similar, and both are macropterous. *Akicera fusca* (Thunberg, 1815) exhibits slight sexual dimorphism. This species possesses the smallest lobe of the group; the lobe of the female is reduced almost to a ridge and the membrane is only slightly depressed. The membrane of the male is more deeply depressed and the lobe is slightly larger. The male is macropterous, the female micropterous.

The following species belonging to the small-lobe group were examined: *Adephagus cristatus* (Burmeister, 1838), *Akicera fusca* (Thunberg, 1815), *Asiotmethis muricatus* (Pallas, 1771), *Atrichotmethis semenovi* (Zubovskij, 1889), *Batrachornis perloides* Saussure, 1884, *Batrachotetrix cantans* Saussure, 1888, *Eremotettix capensis* Miller, 1932, *Filchnerella beicki* Ramme, 1931, *Glyphanus obtusus* Fieber, 1853, *Glyphotmethis heldreichi* (Brunner, 1882), *Prionotropis hystrix* (Germar,

1817), *Pezotmethis tartarus* (Saussure, 1884), *Rhinotmethis hummeli* Sjöstedt, 1933.

Hoplotropis brunneriana Saussure, 1888 is peculiar to the subfamily in that it has no lobe, only a subtympanal ridge. In the sensory structure the posterior projection is absent and the bulbous part smaller. Both sexes are micropterous.

A sound-producing mechanism is found in all genera of *Akicerinae,* but it is often reduced in the females, especially when they are micropterous. The mechanism consists of a specialised venation of the wing, together with a serrate upper edge of the middle tibia.

Most of the species are macropterous, and none are apterous. The micropterous forms are mostly female. Sexual dimorphism of the tympanal organ is not a common feature in this subfamily, unlike *Porthetinae.*

Pamphaginae.

(Fig. 3, *f;* Table 2).

The tympanal organ may be present or absent. All the tympanal organs possess a subtympanal ridge. In some genera the ridge is well defined and some, e. g. *Tropidauchen, Eumigus,* even have tendencies towards forming a lobe. Small traces of a dorsal shell cover exist in some species but this is not a dominant character and is mostly absent. In most genera the membrane is only slightly depressed, sometimes rather more so in the males than in the females. The sclerotic supports of the sensory structure are generally well developed. *Glauia terrea.* I. Bolívar, 1912 has larger sclerotic supports than any other genus.

Sexual dimorphism in the tympanal organ is not usual in this subfamily but is found sometimes.

One female of *Acrostira bellamyi* (Uvarov, 1922) was available for study. This shows peculiarities in that the tympanal organ is very small for the body size. The specimen is apterous and the membrane depressed and slightly sclerotized. A small shell cover is present. The sclerotic supports of the sensory structure are very bulbous, and the membrane is depressed below the level of the body surface, unlike those of most apterous species.

There are three species, *Eunothrotes derjugini* Adelung, 1907, *Paranocarodes straubei* Fieber, 1853 and *Paranothrotes shelkovnikovi* Uvarov, 1918, with the membrane partly or slightly sclerotized and almost

level with the body surface, and the sclerotic supports simplified and poorly developed. These genera are apterous.

The following genera and species studied possess a tympanal organ: *Acinipe crassicornis* I. Bolívar, 1912, *Acrostira bellamyi* Uvarov, 1922, *Eunapiodes latipes* I. Bolívar, 1912, *Eunothrotes derjugini* Adelung, 1907, *Euryparyphes laetus fezanus* Uvarov, 1929, *Glauia terrea* I. Bolívar, 1912, *Glauvarovia mendizabali* Morales Agacino, 1954, *Ocneridia nigropunctata* (Lucas, 1849), *Ocnerodes brunneri* I. Bolívar, 1876, *Ocneropsis bethlemita* I. Bolívar, 1893, *Pamphagus marmoratus* Burmeister, 1838, *Paranocarodes straubei* Fieber, 1853, *Paraeumigus fortius* (I. Bolívar, 1907), *Paranothrotes schelkovnikovi* Uvarov, 1918, *Prionosthenus galericulatus* Stål, 1876, *Tropidauchen marginatum* I. Bolívar, 1912.

Six of the species studied do not possess a tympanal organ; males and females were studied in *Finotia maxima* Jannone, 1938, *Paranocaracris rubripes* (Fischer-Waldheim, 1846) and *Nocarodes serricollis* (Fischer-Waldheim, 1846), and females only in *Araxiana woronowi* (Uvarov, 1918), *Pseudonothrotes levis* Mistshenko, 1951, and *Nocarodes bicoloripes* Uvarov, 1949. All these are apterous or have in the females traces of tegmina only. The absence of a tympanal organ associated with the presence of tegmina (even when very poorly developed) is very rare.

All specimens studied in this subfamily are either micropterous or apterous. Sound-producing mechanisms are unknown.

The tympanal organ has a simpler structure in this subfamily than in *Akicerinae*. Moreover, the tegmina are mostly micropterous type, while those of *Akicerinae* are mostly macropterous.

Ommexechidae.

(Fig. 5, *a*).

In this small family only four species were examined, and only two of them, *Parossa bimaculata* Giglio-Tos, 1894 and *Spathalium hispidum* Brunner, 1900 were found to possess a tympanal organ. The general characters indicate that the membranes are transparent but small and are either slightly depressed or level with the body surface. There is no shell covering, subtympanal lobe or subtympanal ridge.

The membrane of *Parossa bimaculata* is roughly hexagonal with

a point at its upper rim; it is transparent and only slightly depressed posteriorly. The sclerotic supports of the sensory structure are of the *Acrididae* type but generally smaller. They consist of a large folded body, a small stylifom body, a pyriform vesicle and a fusiform body. Ventrally to the sclerotic supports lies a wrinkled sclerotized region. The pyriform vesicle and fusiform body are also surrounded by a slightly sclerotized area as in *Acrididae*. This species is macropterous.

Spathalium hispidum has a poorly developed tympanal organ. The membrane is transparent, roughly the same shape as in *Parossa,* but it is almost level with the body wall. The sclerotic supports are greatly reduced. There are indications only of a pyriform vesicle and fusiform body. A sclerotic cavity is present with a small folded body and styliform body. Males and females are brachypterous.

The brachypterous species *Ommexecha servillei* Blanchard, 1836, and the apterous species *Graea horrida* Philippi, 1863, have no tympanal organs. Although *Ommexechidae* is a very small family there is considerable variety in the structure of the tympanal organ among its genera. In the family as a whole the tympanal organ seems to have poor development, and in some genera it is absent. No sound-producing mechanism has been detected in this family.

Pyrgomorphidae.

(Fig. 4, *a-d;* Table 3).

The tympanal organ may be present or absent. The membrane is roughly D-shaped or circular and is small in relation to body size. In the majority of genera it is transparent and depressed beneath the body surface, the posterior and ventral margin being sunk deeper than the anterior. A subtympanal ridge is generally present. There is no subtympanal lobe or dorsal shell covering, as there is in *Acrididae.*

The sclerotic supports of the sensory structure are of very simple structure. They are represented by one main elongate body extending from the lower anterior corner of the membrane to about half-way towards the centre of it; it is often reduced to a thin line or a convex protruberance as small as a pin head, and sometimes it is absent altogether. Surrounding the supporting body and continuing to the lower anterior margin of the membrane is a weakly sclerotized region.

TABLE 3.

Family PYRGOMORPHIDAE.

Variation of the tympanal organ in relation to tegmen length and presence or absence of a sound-producing mechanism (+ present, — absent).

Tympanal Organ				Wing Development (Number of specimens studied)								Sound-producing mechanism
				Macropterous		Brachypterous		Micropterous		Apterous		
Membrane	Shell cover	Subtympanal lobe	Subtympanal ridge	♂	♀	♂	♀	♂	♀	♂	♀	
Transparent, well developed, depressed	—	—	+	19	17			14	13	1		Not detected
Transparent, not depressed	—	—	weak or absent	1	2	3	2	1	2	1	1	Not detected
Partly sclerotized, poorly developed	—	—	—	1	1			1	3			Not detected
Absent	—	—	—	1	1			3	3	10	12	Not detected

The small membrane, together with the less complex type of sensory structure and the absence of a subtympanal lobe and dorsal shell covering, suggest that *Pyrgomorphidae* have a less developed or a degenerate type of tympanal organ in comparison with other families. Moreover, approximately one-third of the species studied have no trace of tympanal organ. This is the highest proportion of species lacking the tympanal organ in any family or subfamily of *Acridomorpha,* other than those in which its absence is wholly characteristic.

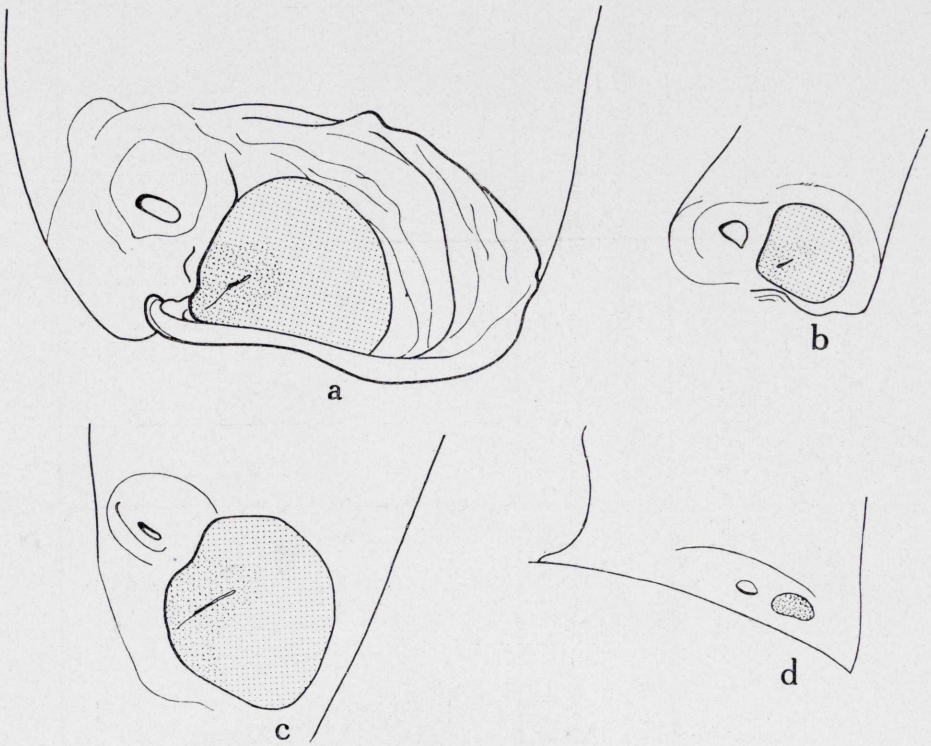


Fig. 4.—*Pyrgomorphidae: a) Phyteumas olivaceus* 1.8 mm.; *b) Stenoxyphus aurantiacus* 0.8 mm.; *c) Aularches miliaris* 1.8 mm.; *d) Caprorhinus zolotarevskyi* (type) 0.5 mm.

The tympanal organ occurs in both macropterous and micropterous species; it is usually absent in apterous species.

No definite sound-producing mechanism was found.

The species can be grouped according to the structure of the tympanal organ, as follows.

The first group have a membrane which is depressed beneath the body surface. A subtympanal ridge is present. As the membrane is

depressed at the ventral margin e. g. *Phyteumas olivaceus* (fig. 4, *a)* the ridge projects more than in any other family. The ridge conceals the lower margin of the membrane, and continues upwards to form an outer rim of the tympanal organ. Between the posterior margin of the membrane and the posterior outer tympanal rim the tergite is sometimes wrinkled; this is a most striking feature absent in other families. The wrinkled region slopes towards the membrane. The depression of the membrane is variable; in species in which it is shallow the subtympanal ridge does not overlap the ventral margin of the membrane, and the tergite is not wrinkled between the outer tympanal rim and the membrane as in *Stenoxyphus aurantiacus* (fig. 4, *b*). There are many intermediate forms between these extreme cases.

The supporting body of the sensory structure is also variable in this group. It may be represented by a slender thickening which is sometimes only a thin white line, or by a small thickening like a pin-head, or it may be absent altogether.

All specimens examined are either macropterous or micropterous; in all cases the tegmina cover the tympanal organ.

The following genera and species belong to this group: *Annandalea robinsoni* I. Bolívar, 1905, *Atractomorpha aurivilii* I. Bolívar, 1884, *Cawendia glabrata* Karsch, 1888, *Chirindites oldendaali* Ramme, 1929, *Chlorizeina unicolor* Brunner, 1893, *Colemania sphenarioides* I. Bolívar, 1910, *Desmoptera truncatipennis* Sjöstedt, 1920, *Humpatella severini* I. Bolívar, 1904, *Kapaoria novaguinea* I. Bolívar, 1898, *Laufferia chloronota* (I. Bolívar, 1889), *Ochrophlebia ligneola* (Serville, 1838), *Ochrophlegma violacea* (Stål, 1876), *Pezotagasta crassipes* Uvarov, 1953, *Phymateus leprosus* (Fabricius, 1793), *Physemophorus sokotranus* (Burr, 1898), *Phyteumas olivaceus* (Karsch, 1896), *Poekilocerus pictus* Fabricius, 1775, *Prosphena scudderi* I. Bolívar, 1884, *Protogasta rosea* I. Bolívar, 1908, *Pseudomorphacris notata* Brunner, 1893, *Pterorthacris subcallosa* Uvarov, 1920, *Pyrgomorpha cognata* Krauss, 1877, *Rubellia nigrosignata* Stål, 1875, *Rutidoderes squarrosus* (Linnaeus, 1771), *Sphenarium mexicanum* Saussure, 1859, *Sphenexia fusiformis* Karsch, 1896, *Stenoscepa granulata* (Karsch, 1888), *Stenoxyphus aurantiacus* Karsch, 1896, *Tagasta indica* I. Bolívar, 1905, *Tanita obesa* Uvarov, 1953, *Taphronota stali* I. Bolívar, 1884, *Yunnanites coriacea* Uvarov, 1924, *Zarytes squalina* I. Bolívar, 1884, *Zonocerus elegans* (Thunberg, 1815).

A second group of species have a membrane which is not depressed

but lies level with the surface of the body. The membrane is also more circular than that of the previous group (see e. g. *Aularches miliaris* (fig. 4, *c*)). The subtympanal ridge is poorly developed or absent. The support of the sensory structure consists of a very slender thickening sometimes only a white line. Macropterous, brachypterous and micropterous species occur in this group, but *Orthacris ceylonica* is the only apterous species studied that possesses a tympanal organ (Table 3). The tegmina in all species cover the tympanal organ.

The following species belong to this group: *Aularches miliaris* (Linnaeus, 1758), *Camoensia insignis* I. Bolívar, 1881, *Dictyophorus spumans* (Thunberg, 1789), *Maura bolivari* Kirby, 1902, *Parapetasia impotens* (Karsch, 1888), *Orthacris ceylonica* Kirby, 1914, *Scutillya verrucosa* Sjöstedt, 1921, *Verdulia dohrni* I. Bolívar, 1905.

A third group of species possess a very small, poorly developed, tympanal structure with a sclerotized membrane.

The membrane of *Caprorhinus zolotarevsky* Uvarov, 1929 (fig. 4, *d*) is level with the surface of the abdomen, and there is no subtympanal ridge and no part of the sensory structure visible externally; this species has very poorly developed tegmina. Three other species, *Chrotogonus homalodemus* (Blanchard, 1836), *Pyrgomorphella arachidis* Dirsh, 1951 and *Phymella capensis* Uvarov, 1922 possess a subtympanal ridge and the membrane is slightly depressed beneath the body wall. The supporting body of the sense organ is difficult to differentiate. These species are micropterous, except *Chrotogonus homalodemus* which is macropterous. Macropterous species are rarely found to have such poorly developed tympanal organs. *Pyrgomorphella arachidis* has tegmina which half cover the tympanal organ, while in *Phymella capensis* the tegmina reach beyond the tympanal organ but do not cover it; in most micropterous species the tegmina cover the tympanal organ.

In a fourth group of species the tympanal organ is absent. Most of these as is usual in *Acridomorpha,* are apterous. However, four species examined possess tegmina: *Popovia salvadore, Leptea debilis* and *Monistria pustulifera* have poorly developed tegmina, and *Tenuitarsus sudanicus* is macropterous. The latter is the only macropterous species without a tympanal organ in the *Pyrgomorphidae* studied.

Sixteen genera and species belong to this group: *Anarchita aptera* I. Bolívar, 1902, *Caconda burri* Kevan, 1951, *Dyscolorhinus squalinus* Saussure, 1899, *Geloius finoti* I. Bolívar, 1905, *Leptea debilis* Finot, 1894, *Mekongiana wardi* Uvarov, 1937, *Monistria pustulifera* Walker.

1871, *Occidentosphena ruandensis* (Rehn, 1914), *Omura congrua* Walker, 1870, *Parasphena pulchripes* Gerstaecker, 1869, *Popovia salvadore* Uvarov, 1950, *Psednura pedestris* Erichson, 1842, *Rakwana ornata* Henry, 1933, *Ramakrishnaia raoi* Kevan, 1953, *Stibarosterna serrata* Uvarov, 1953, *Tenuitarsus sudanicus* Kevan, 1953.

Lentulidae.

The 15 genera and species of the family *Lentulidae* that were studied all lack a tympanal organ. A sound-producing mechanism is also lacking. All are apterous.

Lathiceridae.

The four known genera of this family have no tympanal organ and no known sound-producing mechanism. All are apterous.

Paulinidae.

(Fig. 5, *b*).

A tympanal organ is present in the only examined species *Paulinia acuminata* Blanchard, 1843. The membrane is transparent and roughly oval with a horizontal lower rim. The posterior region is only slightly depressed beneath the surface. There is no shell covering, subtympanal lobe or ridge. Unlike that of most other families, the first abdominal spiracle is very closely connected with the tympanal organ and is slit-like.

The sclerotic supports of the sensory structure consist of a large supporting body (which may represent the folded body), a pyriform vesicle and a fusiform body. This species is macropterous in both sexes. No sound-producing mechanism was detected.

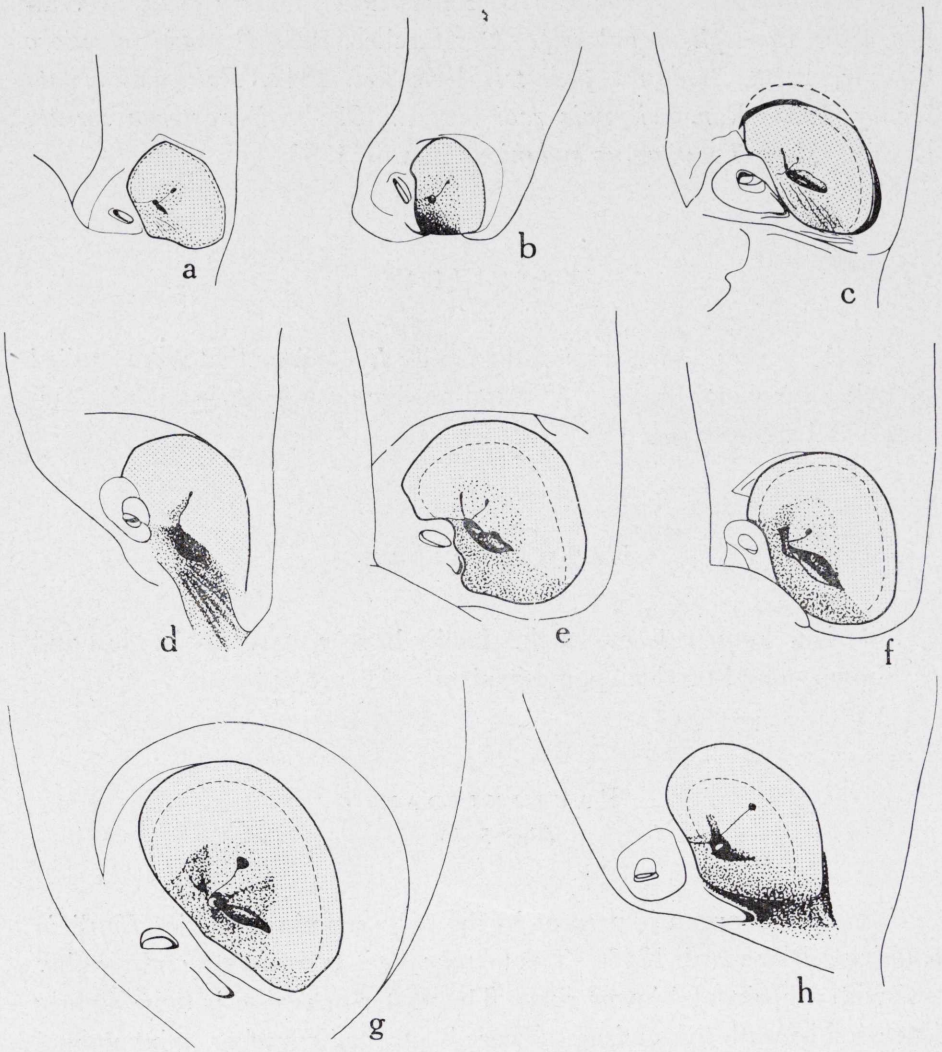


Fig. 5.—*Ommexechidae: a) Parossa bimaculata,* 1.2 mm.; *b) Pauliniidae: Paulinia acuminata,* 0.8 mm.; *c) Dericorythinae: Dericorys philbyi,* 1.8 mm.; *d) Chilacridinae: Philippiacris* sp., 1.2 mm.; *e) Romaleinae: Zoniopoda cruentata,* 2.1 mm.; *f) Procolpia minor,* 2.0 mm.; *g) Acrostegastes affinis,* 1.8 mm.; *h) Eurynotacris somalica,* 1.0 mm.

Acrididae.

(Figs. 5-11, Tables 4-13).

In this large family a tympanal organ may be present or absent. The membrane is usually oval but it may be roughly circular. Most species have a transparent membrane covered by the tegmen, but in

apterous species the membranes are frequently sclerotized. The membrane is generally depressed beneath the cuticle at the dorsal and posterior margin. The depth of the depression is variable and may be relatively great or shallow, or level with the cuticle, as is usual in apterous species. The ventral margin of the membrane is distinct or may merge gradually into a sclerotic folded region of the tergite.

A dorsal shell covering is well developed in some species, but poorly developed or absent in others.

The subtympanal lobe is frequently absent. When it is absent, a subtympanal ridge is usually present or weakly developed.

The sclerotic supports of the sensory structure are fairly uniform. They are situated in the anterior part of the membrane. There is a large elongate folded body whose length is approximately 1/7-1/3 of the largest diameter of the membrane. At the dorsal apex of the folded body there is a small sclerotic cavity; this is an invagination which in *Locusta migratoria migratorioides* (according to Gray 1960) is about 100 μ deep with non-spinous convex projections situated in its deepest region. Dorsally to this is the smaller styliform body, which is roughly circular or sometimes slightly elongated. Near the sclerotic cavity a thin spindle-shaped fusiform body extends towards the centre of the membrane; it varies in length and terminates in a very small pyriform vesicle.

Stridulatory mechanisms are mainly present in this family, but some species that possess a tympanal organ have no detectable sound-producing mechanism. However, sound may be produced in a variety of ways, including a mandibular mechanism which has been reported in various genera of *Acrididae,* e. g. *Heteracris.*

Dericorythinae.

(Fig. 5, *c*).

Only four genera were studied in this subfamily. The tympanal organ is absent in apterous species and present in species with tegmina. The two examined with tegmina, *Dericorys philbyi* Uvarov, 1932 and *Corystoderes escalerai* I. Bolívar, 1936, have similar oval transparent membranes of moderate size and depressed beneath the body surface. Dorsally the cuticle slightly covers the tympanal membrane. There is

no subtympanal lobe, but a ridge is present. The sclerotic supports of the sensory structure are very large and include a large expanded folded body, a relatively large styliform body, and a pyriform vesicle and fusiform body which are of the usual size for *Acrididae*.

Anamesacris abajoi Morales Agacino, 1949 and *Pamphagulus bodenheimeri* Uvarov, 1929 are apterous and do not possess a tympanal organ.

A sound-producing mechanism is unknown except in one species of *Dericorys,* in which a specialisation of wing veins is present.

Chilacridinae.

(Fig. 5, *d*).

Four genera were studied in this small subfamily. A tympanal organ is present in genera with tegmina. The membrane is transparent, with the upper region wider than the lower; it is level with the surface of the body or slightly depressed. The ventral margin of the membrane has an indefinite margin, gradually merging into the tergite as a wrinkled sclerotized region. There is no subtympanal lobe or ridge. The sclerotic supports of the sensory structure are difficult to differentiate clearly in the one membrane available for study. This possesses an unusual bulbous, elongate, folded body, more pronounced than the usual *Acrididae* form, and the pyriform vesicle and fusiform body are present, but the styliform body is only represented by a small more sclerotized area with no definite shape.

Only one female of the macropterous *Chilacris maculipennis* Liebermann, 1943 was available for study but the sensory structure was partly damaged. One male and one female of the micropterous *Phillipiacris* sp. were examined. An apterous female of *Bufonacris walkeri* Kirby, 1871 was found not to possess a tympanal organ.

One male and one female of the brachypterous *Aucacris eumera* Hebard, 1929 were studied. They possess a tympanal membrane depressed at the posterior region and more oval than in the genera already mentioned, and there is a tendency for the upper tympanal rim to overlap the membrane slightly. The ventral margin of the membrane is clearly defined, but there is no subtympanal ridge or lobe. The spiracle is situated slightly further away from the membrane than in

the above genera. The sclerotic supports of the sensory structure are of the usual *Acrididae* type, but in general it appears that this tympanal organ does not belong to the same group as the others studied.

Romaleinae.

(Fig. 5, *e-h;* Table 4).

A tympanal organ is mostly present but may be absent.

The majority of genera have a membrane that is of an irregular circular shape similar to that of *Chilacridinae* with the upper region above the spiracle wider than the lower (e. g. *Zoniopoda cruentata,* fig. 5, *e*); the vertical diameter of the membrane is almost as large as or even larger than the horizontal. The membrane is usually level with the body surface, with the lower rim frequently indistinct owing to ventral folds in the sclerotized region (as in *Eurynotacris somalica,* fig. 5, *h*); because of this the membrane appears to merge gradually into the body surface on the ventral side and there is often complete absence of the subtympanal rim. The subtympanal lobe is usually absent but in a few genera it is poorly developed (e. g. *Procolpia minor,* fig. 5, *f*); in most there is only a ridge which disappears into the sclerotized ventral folds. Running parallel to the edge of the transparent membrane is a white rim. This is an internal supporting structure shoking through the membrane. It is wider and more prominent in *Romaleinae* than in any other subfamily of *Acrididae.* There is no shell covering and there are no well developed lobes; the membrane is completely exposed in every specimen studied.

The sclerotic supports of the sensory structure comprise: a particularly large wide folded body which is raised anteriorly and frequently sunk posteriorly below the membrane surface, an elongate styliform body which may be raised above the surface, a small pyriform vesicle which is often indistinct and a fusiform body which is generally weakly developed ond often not seen.

The genera can be divided into groups according to the presence or absence of the tympanal organ, and when it is present, according to the shape of the membrane, which may be roughly circular or oval. The group containing the majority of genera studied with a roughly circular membrane can be further subdivided into three. Although the

TABLE 4.

Subfamily ROMALEINAE.

Variation of the tympanal organ in relation to tegmen length and presence or absence of a sound-producing mechanism (+ present, — absent).

Tympanal Organ				Wing Development (Number of specimens studied)								Sound-producing mechanism
				Macropterous		Brachypterous		Micropterous		Apterous		
Membrane	Shell cover	Subtympanal lobe	Subtympanal ridge	♂	♀	♂	♀	♂	♀	♂	♀	
Roughly circular: Transparent, slightly depressed	—	—	+	1	1							+
Transparent, not depressed	—	slight	—	1	2	1	1					+
Transparent, not depressed	—	—	weak or absent	15	14	2	6	2	3			+
Oval: Transparent, slightly depressed	—	—	+ or —	1	1			3	3			+
Absent	—	—	—							2	2	None detected

differences in these groups are relatively small the characteristic tendencies are interesting, and reveal the main trend of the subfamily.

Among the three smaller groups *Tytthotyle maculata* is best placed into a group of its own, as the membrane is slightly depressed beneath the body surface, and this is the only species studied with a roughly circular and also depressed membrane.

The second smaller group possesses membranes that are not depressed beneath the body surface, but a poorly developed subtympanal lobe is present. There are three species in this group: *Dracotettix monstrosus* Bruner, 1889, *Procolpia minor* Giglio-Tos, 1894, *Prorhachis granulosa* Scudder, 1875.

In the third group, containing the majority of genera studied, the membrane is not depressed beneath the body surface and there are no traces of a subtympanal lobe. In this group *Brachystola magna* has some peculiarities in that the ventral margin of the membrane has a definite edge and does not gradually marge into folds, the folded body is less developed, and no fusiform body or pyriform vesicle was detected though the stylform body is of the normal type as described above, and the membrane is very small.

Most of the genera in this third group are macropterous or brachypterous. The following genera and species were studied: *Aeolacris bella* Rehn, 1909, *Agriacris triliniata* (Serville, 1831), *Alcamenes cristatus* Bruner, 1906, *Aplatacris lepreosus* I. Bolívar, 1881, *Brachystola magna* (Girard, 1853), *Callonotacris lophophora* Rehn, 1909, *Chromacris miles* (Drury, 1773), *Cibotopteryx variegata* Rehn, 1905, *Colpolopha obsoleta* (Serville, 1831), *Draconata mancus* Pictet & Saussure, 1887, *Eutropidacris callaris* (Stoll, 1813), *Homalosaparus canonicus* Rehn, 1908, *Lophacris humboldtii* (Scudder, 1869), *Munatia decorata* Carl, 1916, *Phrynotettix tsivavensis* (Haldeman, 1852), *Prionacris coerulescens* (I. Bolívar, 1890), *Prionolopha serrata* (Linnaeus, 1758), *Romalea microptera* (Beauvois, 1805), *Taeniopoda eques* (Burmeister, 1838), *Titanacris carinata* (Stoll, 1813), *Tropidacris grandis* (Thunberg, 1824), *Tytthotyle maculata* (Bruner, 1889), *Xestotrachelus* sp., *Xyleus laevipes* Stål, 1878, *Zoniopoda cruentata* (Blanchard, 1837).

Two species, *Antandrus viridis* Blanchard, 1851 and *Tropidostethus bicarinatus* Philippi, 1863, have no tympanal organ. They are apterous.

All the species mentioned above are from America, while those below are from Africa and Asia.

These have oval-shaped membranes of the usual *Acrididae* type which are slightly depressed posteriorly (as e. g. *Acrostegastes affinis,* fig. 5, *g*). There are no dorsal shell coverings and also no subtympanal lobes. The ventral edge of the membrane is distinct and is sometimes raised above the body surface. A ridge is faintly present in some species but completely absent in others. The sclerotic supports of the sensory structure are of the usual *Acrididae* type with a well developed fusiform body and pyriform vesicle, but variation is found in the styliform body which in some species is small and elongate and in others large and splayed out. All species are micropterous except the macropterous *Teratodes monticollis.* Genera and species studied are: *Acrostegastes affinis* Karsch, 1896, *Kabulia balucha* Uvarov, 1931, *Pelecinotus brachypterus* I. Bolívar, 1902, *Teratodes monticollis* (Gray, 1832).

The method of stridulation, with specialized veinlets, which is a subfamily character (Dirsh, 1961), is present in all genera except the two which are apterous. Although the stridulatory mechanism is identical throughout the subfamily, there is variety in the morphology of the tympanal organ and the sensory structure. The membrane is slightly more depressed and the pyriform vesicle and fusiform body more distinct in the species of the Old World than in those of the New.

Lithidiinae.

Only three genera were studied in this small subfamily. *Lithidium pusillum* Uvarov, 1925 and *Lithidiopsis carinatus* Dirsh, 1956 are both apterous. The male of *Microtmethis kuthyi* Karny, 1910 is macropterous and the female brachypterous. Tympanal organs are absent in all genera. Sound-producing mechanisms are unknown.

Hemiacridinae.

(Fig. 6, *a-f;* Table 5).

A tympanal organ is usually present but may be very poorly developed or absent. The membrane is oval, generally transparent and depressed beneath the body surface at the upper anterior and posterior margins. The dorsal tympanal rim frequently develops into a shell-like

covering overlapping the membrane. There is no subtympanal lobe. A subtympanal ridge is present, but sometimes only weakly developed. The sclerotic supports of the sensory structure are of the usual *Acrididae* type. The styliform body varies in different genera and species; it is generally an elongate process about one-third the length of the folded body (as e. g. *Mesopsera filum*, fig. 6, *b*, *e*) but sometimes it is large and circular. The pyriform vesicle is larger and more distinct than in *Romaleinae*. The sclerotic supports are often absent, particularly if the membrane is sclerotized or poorly developed.

Tympanal organs with a shell covering occur mainly in macropterous species. Apterous species usually do not possess a tympanal organ; if present in them, it is very poorly developed (fig. 6, *d*).

Four groups of genera are recognised according to the structure of the tympanal organ. The first group possesses a thin shell-like covering which overlaps the dorsal region of the membrane. The devolopment of the shell covering is variable and when the membrane is more deeply depressed the covering is larger, sometimes overlapping as much as three-quarters of the membrane. The aperture between the edge of the shell and the membrane is narrow. One of the largest shell covering is found in *Sudanacris pallida* (fig. 6, *a*), in which it hides the upper anterior and a major part of the posterior margin. The upper margin is tilted into the body wall to an appreciable depth, more so posteriorly than anteriorly. Some species possess only a small shell covering (as e. g. *Mesoptera filum*, fig. 6, *b*), and there are many intermediate forms. *Oraistes luridus* differs from other genera in this subfamily in having a wider opening between the edge of the shell and the membrane. In most cases the subtympanal ridge is present, but it may be only weakly developed, gradually facing into the ventral folds beneath the membrane. The ventral margin of the membrane near and below the horny process often lies slightly above the general body surface. The sclerotic supports of the sensory structure are as described above; *Pareuthymia fusca* (fig. 6, *f*) has a particularly elongate styliform body. The species studied are mainly macropterous; *Mesopsera filium* is brachypterous and *Xenippa viridula* micropterous.

The species studied in this group are as follows: *Acanthoxia gladiator* Westwood, 1841, *Clonacris kirbyi* (Finot, 1930), *Gonyacanthella lanceolata* I. Bolívar, 1890, *Hemiacris fervens* Walker, 1870, *Leptacris violacea* (Karny, 1907), *Mesopsera filum* I. Bolívar, 1890, *Oraistes luridus* Karsch, 1896, *Pareuthymia fusca* Willemse, 1930, *Phalinus*

rammei Uvarov, 1953, *Spathosternum prasiniferum* (Walker, 1870), *Pristocorypha* sp., *Sudanacris pallida* (Burmeister, 1838), *Thymiacris multicolor* Willemse, 1937, *Xenippa viridula* Stål, 1878, *Zygoclistron trachystictum* Rehn, 1905.

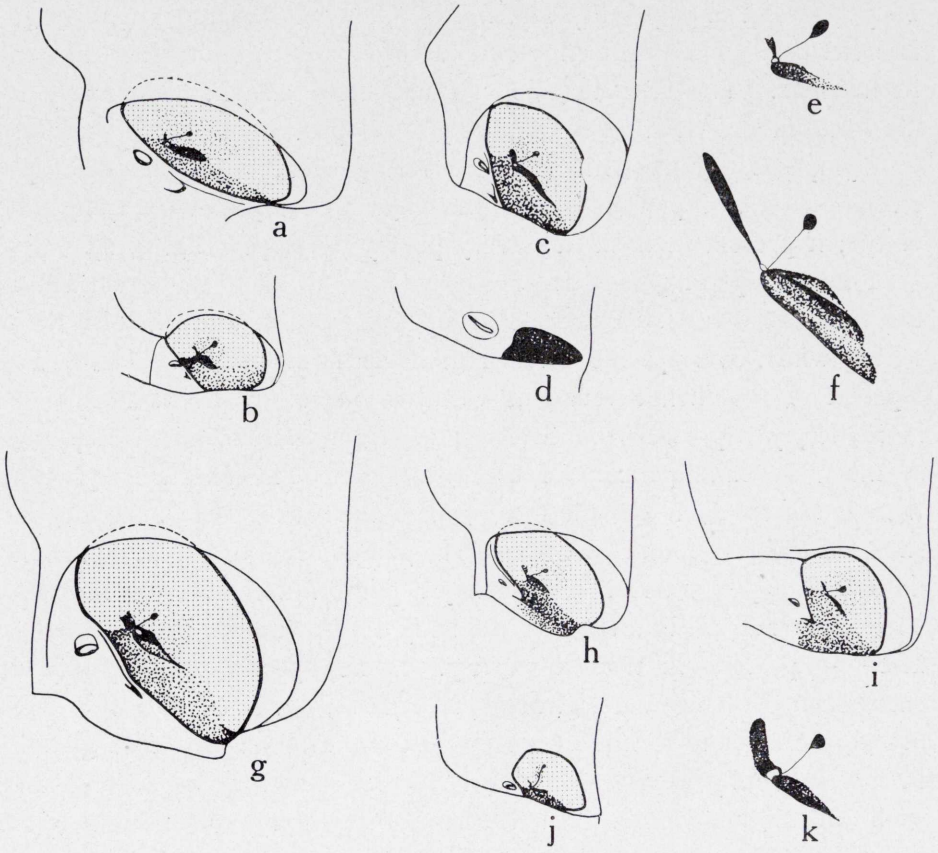


Fig. 6.—*Hemiacridinae: a) Sudanacris pallida,* 2.0 mm.; *b) Mesopsera filum,* 1.1 mm.; *c) Paratraulia karnyi,* 1.8 mm.; *d) Zeylonacris cingalensis,* 1.0 mm. Sclerites of sense organ: *e) Mesopsera filum; f) Pareuthymia fusca. Tropidopolinae: g) Afroxyrrhepes procera,* 2.2 mm.; *h) Tropidopola cylindrica,* 1.6 mm.; *i) Dabba bampura,* 1.2 mm.; *j) Bambusacris greeni,* 0.7 mm. External sclerites of sense organ: *k) Tristria dimorpha.*

The species of the second group possess a tympanal organ without a shell covering, though some of the macropterous forms have a very slight tendency towards this. The membrane is shallowly depressed at the upper, anterior and posterior margins. In most cases the ventral margin of the membrane is level with the body surface and is not raised above it. The majority of genera possess a subtympanal ridge,

TABLE 5.

Subfamily HEMIACRIDINAE.

Variation of the tympanal organ in relation to tegmen length and presence or absence of a sound-producing mechanism (+ present, — absent).

Tympanal Organ				Wing Development (Number of specimens studied)								Sound-producing mechanism
				Macropterous		Brachypterous		Micropterous		Apterous		
Membrane	Shell cover	Subtympanal lobe	Subtympanal ridge	♂	♀	♂	♀	♂	♀	♂	♀	
Transparent, moderately depressed	+	—	+ or —	12	12	1	2	1	1			+
Transparent, shallowly depressed	—	—	+ or —	9	7	1	3	3	4			+
Not depressed sclerotized	—	—	—						2	1	1	None detected
Absent	—	—	—							3	3	None detected

but in some it is weakly developed. Generally the males and females of the same species have similar tympanal organs, but in *Paraspathosternum pedestris* the membrane is deeper posteriorly in the male than in the female. In *Glauningia macrocephala,* the female shows tendencies to a small shell covering while the membrane of the male is slightly more depressed than that of the female but has no shell covering. *Malagasacris strateia* has a membrane which is only slightly depressed, and there is no definite edge to the membrane and no definite ridge. The sclerotic supports are as described above for the subfamily. The species belonging to this group may be macropterous, brachypterous or micropterous; those studied are as follows: *Aleuas lineatus* Stål, 1878, *Bermius brachycerus* Stål, 1828, *Castetsia dispar* I. Bolívar, 1902, *Coloracris azureus* Willemse, 1938, *Gesonula sanguinolenta* Krauss, 1902, *Glauningia macrocephala* Ramme, 1929, *Hieroglyphus oryzivorus* Carl, 1916, *Lopheuthymia brunneri* (Finot, 1907), *Kassongia flavovittata* I. Bolívar, 1908, *Loryma perficita* (Walker, 1870), *Malagasacris strateia* Rehn, 1944, *Parahieroglyphus bilineatus* (Kirby, 1914), *Paraspathosternum pedestris* (Miller, 1929), *Paratraulia karnyi* Willemse, 1925, *Pseudocarsula tarsalis* (Walker, 1870), *Willemsella bicolor* Miller, 1934.

The third group contains only three species. The membrane is sclerotized or poorly developed and very small; it is not depressed. The species are either micropterous or apterous. In *Perakia maculipennis* Ramme, 1930 there are only small vestiges of the sensory structure and in the apterous species *Zeylonacris cingalensis* Kirby, 1914 there is no trace of it. In the female, the tympanal organ is completely absent. Only one female was studied and this is micropterous.

The fourth group of species have no tympanal organs in either sex and are apterous. Only three species were studied: *Calviniacris nudus* Dirsh, 1955, *Leatettix laticornis* Dirsh, 1956 and *Uvarovidium peninsulare* Dirsh, 1956.

Sound-producing mechanisms are generally present in *Hemiacridinae,* in the form of specialized veinlets, but are less pronounced in brachypterous species; in micropterous and apterous forms they are unknown.

TROPIDOPOLINAE.

(Fig. 6, *g-k;* Table 6).

A tympanal organ is present in all genera studied. The membrane is transparent, generally depressed posteriorly and oval. A dorsal shell covering is usually present but occasionally absent. The subtympanal ridge is well developed.

The subfamily may be divided into three groups (Table 6) according to the depression of the membrane and the presence or absence of the shell covering.

The first group consists of species with the membrane deeply depressed at the dorsal and posterior margin (as e. g. in *Afroxyrrhepes procera,* fig. 6, *g*), with the antero-ventral margin raised above the body surface. The dorsal shell covering is large and there is a wide aperture between the shell and the membrane, the width of which is approximately half the diameter of the membrane. The sclerotic supports of the sensory structure are of the normal *Acrididae* type; the styliform body is roughly circular and large, or narrow and elongate. All species are macropterous.

The species in this group examined are: *Afroxyrrhepes procera* Burmeister, 1838, *Chloroxyrrhepes virescens* (Stål, 1873), *Homoxyrrhepes punctipennis* (Walker, 1870), *Oxyrrhepes extensa* (Walker, 1859), *Petamella prosternalis* (Karny, 1907).

The second group of species possess a membrane that is shallowly depressed posteriorly and not raised above the surface at the anterior ventral margin; in some species the antero-ventral margin of the membrane is ill-defined (as e. g. in *Tropidopola cylindrica obtusa,* fig. 6, *h*). A dorsal shell covering is present, but the aperture between the shell and the membrane is narrow, being less than half the diameter of the membrane. *Tristria dimorpha* (fig. 6, *k*) has a larger styliform body than the other species studied. The species in this group are macropterous, brachypterous or micropterous. There are no apterous specimens available for study in this subfamily.

The species in this group examined are: *Calamippa prasina* I. Bolívar, 1940, *Limnippa ensicerca* Uvarov, 1941, *Mesopsilla roseoviridis* Ramme, 1929, *Tinnevellia andrewi* Henry, 1940, *Tristria dimorpha* I. Bolívar, 1912, *Tropidopola obtusa* Uvarov, 1922.

The third group consists of two genera, in which the membrane

TABLE 6.

Subfamily TROPIDOPOLINAE.

Variation of the tympanal organ in relation to tegmen length and presence or absence of a sound-producing mechanism (+ present, — absent).

Tympanal Organ				Wing Development (Number of specimens studied)								Sound-producing mechanism
				Macropterous		Brachypterous		Micropterous		Apterous		
Membrane	Shell cover	Subtympanal lobe	Subtympanal ridge	♂	♀	♂	♀	♂	♀	♂	♀	
Transparent, deeply, depressed	+	—	+	5	5							None detected
Transparent, shallowly depressed	+	—	+	3	3	1	1	2	2			ditto
Transparent, not or only very slightly depressed	—	—	+		1			1	1			ditto

is level or almost level with the cuticle. There is no shell covering. *Bambusacris greeni* Henry, 1939 (fig. 6, *j*) is micropterous and has a very small styliform body and a very long folded body; and *Dabba bampura* Uvarov, 1933 (fig. 6, *i*) is macropterous. No sound producing mechanism was found.

Oxyinae.

(Fig. 7, *a-d;* Table 7).

A tympanal organ is present in all species examined. The membrane is very uniform, mostly transparent, with a tendency towards a more circular outline than in previous subfamilies. It is usually slightly depressed posteriorly as in most *Acrididae*. There is no subtympanal lobe but a subtympanal ridge is present. There is also no shell-covering and the membrane is therefore completely exposed (*Oxya adentata*, fig. 7, *a*) except that it is generally covered by the tegmen. The sclerotic supports of the sensory structure are fairly uniform and frequently black. The pyriform vesicle is generally comparatively large and distinct. In *Caryanda spuria* (fig. 7, *d*), *Dapperia bermioides* and *Austeniella cylindrica* the styliform body is large, while in *Genditia versicolor* (fig. 7, *c*) it is small. In some cases (e. g. *Ochrolandriphaga*) the ventral margin of the membrane is indistinct and gradually merges with the tergite. The membrane is usually the same in both male and female, but in *Genditia versicolor* it is slightly more depressed in the male than in the female. Most of the specimens studied are micropterous, but there are also macropterous and brachypterous species.

The following species have a membrane which is depressed: *Austeniella cylindrica* Ramme, 1929, *Badistica bellula* Karsch, 1891, *Caledonula fuscovittata*, 1923, *Caryanda spuria* Stål, 1860, *Cercina obtusa* Stål, 1878, *Chitaura indica* Uvarov, 1929, *Dapperia bermioides* Sjöstedt, 1921, *Dibastica* sp., *Genditia versicolor* (Ramme, 1929), *Lucretilis uvarovi* Miller, 1935, *Ochrolandriphaga xanthelytrana* Henry, 1935, *Oxya adentata* Willemse, 1925, *Quilta oryzae* Uvarov, 1926, *Racilia aurora* Brunner Wattenwyl, 1893, *Zulua glabra* Ramme, 1929.

There are two species *Digentia fasciata* Ramme, 1929 and *Pterotiltus impennis* Karsch, 1891 (fig. 7, *b*) in which the membrane is level

with the body surface, more circular than in the genera listed above, slightly sclerotised and not covered by the poorly developed tegmen.

No sound-producing mechanisms were detected in this subfamily.

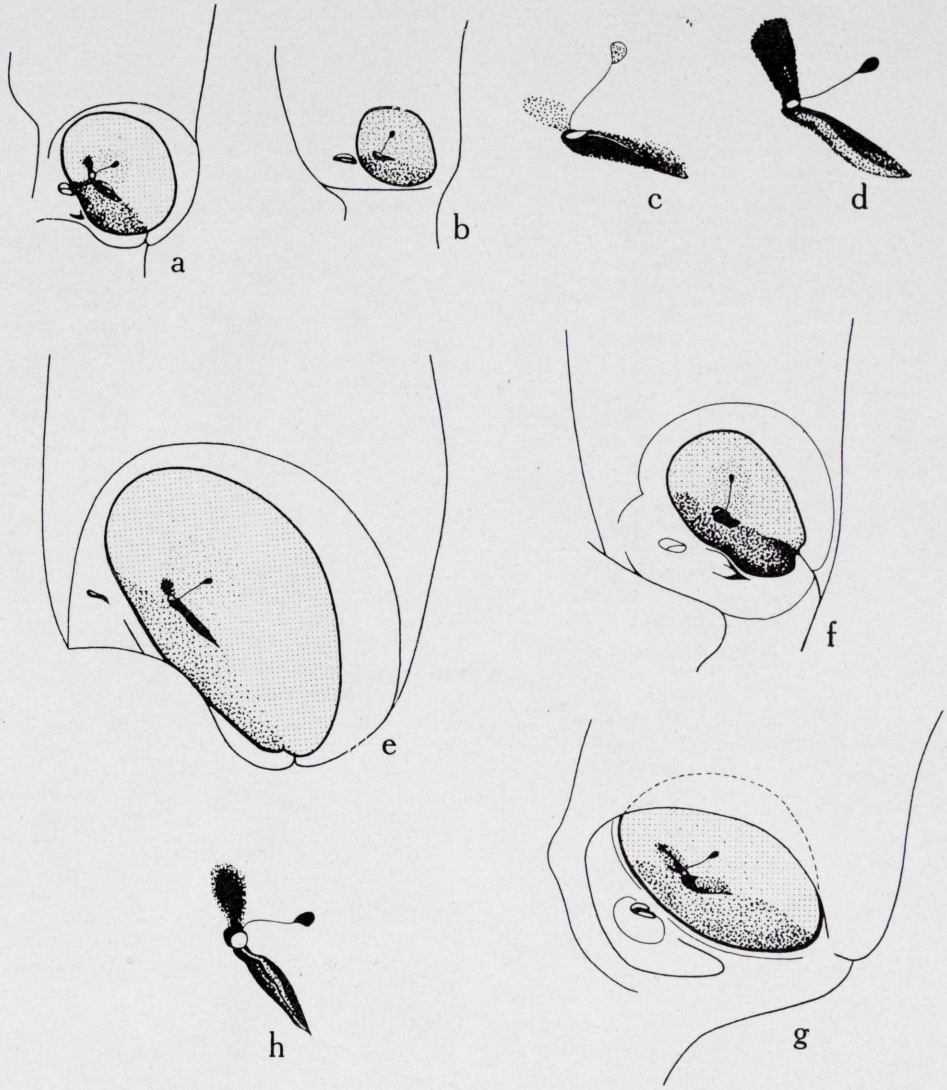


Fig. 7.—*Oxyinae: a) Oxya adentata,* 1.0 mm.; *b) Pterotiltus impennis,* 1.1 mm. Sclerites of sense organ: *c) Genditia versicolor; d) Caryanda spuria. Coptacridinae: e) Coptacra ensifera,* 1.7 mm.; *f) Ruwenzoracris fasciata,* 0.8 mm.; *g) Dubitacris robustus,* 1.2 mm. Sclerites of sense organ: *h) Traulia azureipennis.*

TABLE 7.

Variation of the tympanal organ in relation to tegmen length and presence or absence of a sound-producing mechanism (+ present, — absent).

Subfamily	Tympanal Organ				Wing Development (Number of specimens studied)								Sound-producing mechanism
					Macropterous		Brachypterous		Micropterous		Apterous		
	Membrane	Shell cover	Subtympanal lobe	Subtympanal ridge	♂	♀	♂	♀	♂	♀	♂	♀	
Oxyinae	*Circular:* Transparent, shallowly depressed	—	—	+	4	4	1		9	8			None detected
	Slightly sclerotized, level with body surface	—	—	+					2				ditto
Coptacridinae	*Oval:* Transparent, shallowly depressed	Absent or slight	—	+	9	9	1	1	1	1			ditto
	Slightly sclerotized, almost level with body surface	—	—	+					1	1			ditto
	Transparent, shallowly depressed	+	—	+					1	1			ditto

Coptacridinae.

(Fig. 7, *e-h;* Table 7).

All specimens studied possess a tympanal organ. The membrane is usually transparent, oval and slightly depressed at the posterior margin (as e. g. in *Coptacra ensifera,* fig. 7, *e*); it is very uniform throughout the group. A subtympanal ridge is present which tends towards a small lobe but this is only weakly developed. There is no well developed shell-covering but some genera (e. g. *Poecilocerastis, Exochoderes)* show tendencies towards one. The sclerotic supports of the sensory structure are uniform and of the typical *Acrididae* type. The styliform body is generally circular and small, but in *Traulia azureipennis* (fig. 7, *h*) it is particularly large.

Ruwenzoracris fasciata (fig. 7, *f*), which is micropterous, has a membrane which is level with the abdomen surface and slightly sclerotized. The sclerotic supports are extremely small. Generally the membranes of male and female are similar but in *Paracoptacra cauta* the membrane is slightly more depressed in the male.

Dubitacris robustus (fig. 7, *g*) is unique in the subfamily in that it possesses a well developed shell covering. Also the ventral margin of the membrane is slightly raised above the surface, and the styliform body is fairly large. Although this species is micropterous the tympanal organ appears to be the most highly developed in the subfamily, which suggests that it may belong to another subfamily.

Most of the genera are macropterous, but there are also brachypterous and micropterous genera. No sound-poducing mechanism is known.

Species studied are: *Apalacris varicornis* (Walker, 1810), *Bocagella bolivari* Miller, 1932, *Coptacra ensifera* I. Bolívar, 1902, *Cyphocerastis tristis* Karsch, 1891, *Dubitacris robustus* Henry, 1938, *Epistaurus sinetyi* I. Bolívar, 1902, *Eucoptacra saturata* Walker, 1870, *Exochoderes aurantiacus* I. Bolívar, 1881, *Paracoptacra cauta* Karsch, 1896, *Parepistaurus stigmaticus* I. Bolívar, 1912, *Poecilocerastis tricolor* (I. Bolívar, 1912), *Ruwenzoracris fasciata* Ramme, 1929, *Traulia azureipennis* (Serville, 1839).

Calliptaminae.

(Fig. 8, *a-d;* Table 8).

A tympanal organ is present in all genera and species studied. The membrane is transparent, oval and moderately depressed at the posterior margin. A small subtympanal lobe is usually present (as e. g. in *Calliptamus italicus,* fig. 8, *b*) but it may be absent in micropterous species, in which case a well defined ridge is present. A shell covering

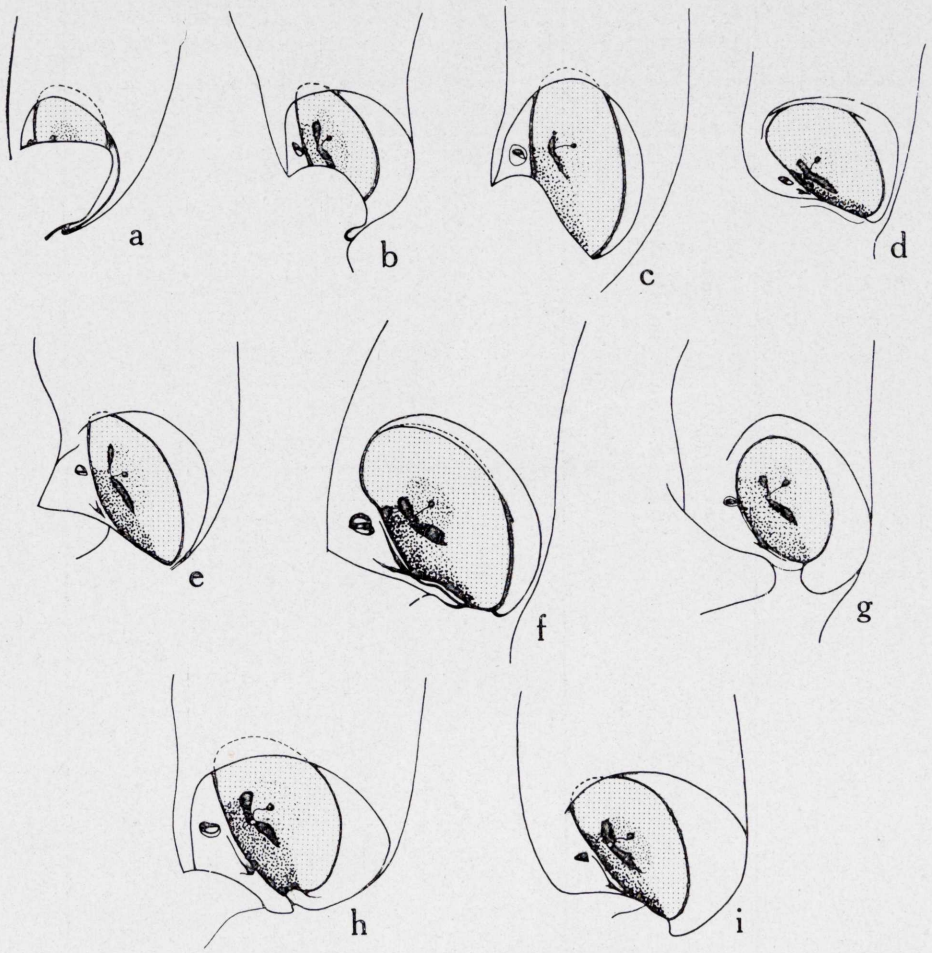


Fig. 8.—*Calliptaminae: a) Acorypha picta,* 1.4 mm.; *b) Calliptamus italicus,* 2.0 mm.; *c) Brachyxenia scutifera,* 2.4 mm.; *d) Paracaloptenus caloptenoides,* 1.7 mm.; *Euryphyminae: e) Euryphymus tuberculatus,* 1.8 mm.; *f) Acrophymus cuspidatus,* 2.7 mm.; *g) Surudia loboptera,* 1.4 mm.; *Eyprepocnemidinae: h) Eyprepocnemis plorans ibandana,* 1.7 mm.; *i) Pareuprepocnemis syriaca,* 1.7 mm.

TABLE 8.

Variation of the tympanal organ in relation to tegmen length and presence or absence of a sound-producing mechanism (+ present, — absent).

Subfamily	Tympanal Organ				Wing Development (Number of specimens studied)								Sound-producing mechanism
	Membrane	Shell cover	Subtympanal lobe	Subtympanal ridge	Macropterous		Brachypterous		Micropterous		Apterous		
					♂	♀	♂	♀	♂	♀	♂	♀	
Calliptaminae	Transparent, moderately depressed	+	+	—	7	7							Not sufficiently studied
	Transparent, moderately depressed	small	—	+					4	4			None detected
Euryphyminae	Transparent, moderately depressed	Present, but sometimes slight	—	+	10	10	1	2	1	1			None detected
	Transparent, shallowly depressed	—	—	weak					1	1			None detected

is present in all species but more developed in those with a subtympanal lobe. The sensory structure is uniform throughout the subfamily and of the usual *Acrididae* type.

The *Calliptaminae* can be grouped according to the development of the shell covering and of the lobe. In the first group the membrane is fairly depressed, but the shell covering does not cover a large proportion of the membrane and the lobe generally covers only a part of the sclerotic supports of the sensory structure; *Acorypha picta* (fig. 8, *a*) has the largest lobe, which covers the sclerotic supports. *Brachyxenia scutifera* (fig. 8, *c*) has the least developed lobe. All species examined are macropterous.

Species belonging to this group are: *Acorypha picta* Krauss, 1877, *Bothrocaracris bolivari* Uvarov, 1960, *Brachyxenia scutifera* (Walker, 1870), *Calliptamus italicus* (Linnaeus, 1758), *Stobbea riggenbachi* Ramme, 1929, *Sphodromerus tuareg* Uvarov, 1941, *Sphodronotus cyclopterus* Uvarov, 1933.

A second group comprises four genera and species of those examined. There is a small shell covering but no subtympanal lobe; the membrane is transparent and moderately depressed posteriorly; it has a definite edge ventrally and in this region is slightly raised above the body surface. A well defined subtympanal ridge is present, but is does not overlap the membrane. The sclerotic supports of the sensory structure are similar to those of the previous group. All species are micropterous.

Species examined are: *Indomerus noxius* Dirsh, 1951, *Palaciosa khandalensis* I. Bolívar, 1900, *Paracaloptenus caloptenoides* Brunner Wattenwyl, 1861, *Peripolus pedarius* Stål, 1878.

From the descriptions above it is evident that the larger development of the shell covering and the lobe occurs in macropterous species, while species with a smaller shell covering and with a subtympanal ridge but no lobe are micropterous (Table 8).

There is no record of a stridulatory mechanism.

Euryphyminae.

(Fig. 8, *e-g;* Table 8).

A tympanal organ is present in all of the species examined. The membrane is very uniform in the subfamily, being oval, transparent

and generally moderately depressed posteriorly. A small shell covering is present in most genera. A subtympanal ridge is present in all species, but there is no lobe. The sclerotic supports of the sensory structure show little variation.

The genera may be divided into groups according to the degree of depression of the membrane. Most of the species examined are in the first group, with a moderately depressed membrane and a small shell covering. The development of the shell covering varies; one of the most developed is in *Euryphymus tuberculatus* (fig. 8, *e*) while other species such as *Acrophymus cuspidatus* (fig. 8, *f*), *Aneuryphymus erythropus, Brachyphymus vylderi* and *Pachyphymus cristulifera* have only a slight shell covering. In *Plegmapterus saturatus,* the subtympanal ridge is better developed in the male than in the female.

The majority of species of this group are macropterous, but two are brachypterous and one micropterous. Those studied are: *Acrophymus cuspidatus* Karsch, 1900, *Amblyphymus miniatus* Uvarov, 1922, *Anabibia thoracica* Dirsh, 1956, *Aneuryphymus erythropus* (Thunberg, 1815), *Brachyphymus vylderi* Stål, 1876, *Calliptamicus semiroseus* (Serville, 1838), *Calliptamulus sulfurescens* Uvarov, 1922, *Euryphymus tuberculatus* Martínez, 1898, *Pachyphymus cristulifera* (Serville, 1838), *Phymeurus granulatus* (Uvarov, 1922), *Platacanthoides bituberculatus* Uvarov, 1922, *Plegmapterus saturatus* Walker, 1870, *Rhachitopis ceraseus* Uvarov, 1922.

The second group contains only one species, *Surudia loboptera* Uvarov, 1930, (fig. 8, *g*), with a very shallowly depressed membrane and no trace of shell covering. The subtympanal ridge is weakly developed. This species is micropterous.

No sound-producing mechanism is known.

Eyprepocnemidinae.

(Fig. 8, *h-i;* Table 9).

A tympanal organ is present in all genera studied. The membrane is well developed, oval and generally depressed posteriorly, and a shell covering is usually present. The posterior margin of the shell covering widens basally (as e. g. in *Eyprepocnemis plorans ibandana,* fig. 8, *h*) and becomes slightly raised above the level of the second abdominal segment. A subtympanal ridge is present; in some cases it is well

defined and may be called a poorly developed lobe. In most genera and species the ventral margin of the membrane is clearly distinguishable.

The sclerotic supports of the sensory structure include a styliform body which, in most species, is very large, flat and roughly circular or slightly oval, and may be as large as or larger than the folded body; the folded body, fusiform body and pyriform vesicle are all clearly visible.

The species examined can be divided into three groups according to the degree of depression of the tympanal membrane, but a gradual transition from one group to another is evident.

In the first group the membrane is very deeply depressed into the body surface so that the aperture is much wider than that found in *Hemiacridinae* and the shell cover is a much thicker structure. The perpendicular distance from the membrane to the edge of the shell is three-quarters of the greatest width of the membane, so that the edge of the shell forms approximately half a circle. The tegmina in this group are mainly macropterous but may be brachypterous.

Genera and species examined in this group are: *Amphiprosopia adjuncta* Walker, 1810, *Belonocnemis elegantulus* I. Bolívar, 1914, *Cataloipus cognatus* (Walker, 1870), *Choroedocus illustris* (Walker, 1870), *Cyathosternum roseus* I. Bolívar, 1914, *Eyprepocnemis plorans* (Charpentier, 1825), *Eupreponotus inflatus* Uvarov, 1921, *Heteracris speciosa* Sjöstedt, 1913, *Jucundacris pictipes* (Walker, 1870), *Navasia insularis* Kirby, 1914, *Phyllocerus bicoloripes* Uvarov, 1941, *Tylotropidius patagiatus* (Karsch, 1893), *Thisoicetrinus pterostichus* (Fischer-Waldheim, 1833), *Tropidiopsis pendulus* (Karsch, 1896).

In the species of the second group the membrane is only moderately depressed and the shell covering is less pronounced, as e. g. in *Pareuprepocnemis syriaca* (fig. 8, *i*). The majority of species are micropterous but some are macropterous. Genera and species belonging to this group are: *Cyclopternacris cincticollis* (Walker, 1870), *Eucnemidia charlottae* Ramme, 1941, *Macrotona australis* Walker, 1870, *Macrocara picta* Sjöstedt, 1921, *Oxyaeida poultoni* Ramme, 1929, *Parathisoicetrus aethiopicus* Ramme, 1929, *Pareuprepocnemis syriaca* Brunner Wattenwyl, 1861, *Taramassus cunctator* (Karsch, 1900).

Two of the species examined constitute a third group; these are *Asmara glabra* Uvarov, 1937 and *Habrocnemis shanensis* Uvarov, 1943. The membrane is only very shallowly depressed and there is no shell

TABLE 9.

Subfamily EYPREPOCNEMIDINAE.

Variation of the tympanal organ in relation to tegmen length and presence or absence of a sound-producing mechanism (+ present, — absent).

Tympanal Organ				Wing Development (Number of specimens studied)								Sound-producing mechanism
				Macropterous		Brachypterous		Micropterous		Apterous		
Membrane	Shell cover	Subtympanal lobe	Subtympanal ridge	♂	♀	♂	♀	♂	♀	♂	♀	
Transparent, deeply, depressed	+	—	+	12	13		1					Mandibular
Transparent, moderately depressed	Present, but sometimes slight	—	+	3	2			5	5			Mandibular
Transparent, almost level	—	—	+					2	2			None detected

cover present. In *Habrocnemis shanensis* the margin of the membrane is indistinct. Both genera are micropterous.

From the above descriptions of the groups it can be seen that in general the macropterous and brachypterous species have the most deeply depressed membrane (Table 9). There are no apterous species in this subfamily.

In *Taramassus cunctator, Tropidiopsis pendulus, Thisoicetrinus pterostichus* and *Choroedocus illustris,* the subtympanal ridge tends towards a lobe.

Stridulatory mechanisms were not found, but sound production by the mandibles is known in some species.

Catantopinae.

(Fig. 9, *a-i;* Table 10).

This subfamily is rather mixed from the taxonomic point of view.

Males and females from 245 genera and species have been studied. A tympanal organ is generally but not invariably present. The membrane is usually transparent, oval, and depressed beneath the body surface at the posterior margin but often raised slightly at the lower anterior margin. In some species the membrane is more circular and in others again it is small, of irregular shape and sclerotized. A shell cover may be present or absent. There is no subtympanal lobe.

According to the characters of the tympanal organ, the species can be divided into five groups. The first group has an approximately oval transparent membrane which is moderately depressed beneath the cuticle. (No very deeply depressed membrane occurs in this subfamily). A shell cover is always found, generally of moderate development (as e. g. in *Catantops melanostictus* Schaum, 1853, fig. 9, *a*); however, in *Ischnansis curvicerca* Uvarov, 1938 the shell cover conceals a very large part of the membrane. The shell cover is more prominent in the group *Catantopes.* Most of the species are macropterous.

The second group have shallowly depressed transparent membranes. The shell cover is present but in a very reduced form (as in *Leptysma marginicollis* Serville, 1839, (fig. 9, *b*) and in extreme cases as only a tendency. Most species are macropterous or micropterous. Apterous species of this subfamily do not possess a shell covering.

The third group have a transparent membrane, frequently more

circular, and with very little depression at the posterior margin or none. There is no trace of shell covering (e. g. *Podisma pedestris* (Linnaeus, 1758), fig. 9, *c*). The species are mainly micropterous or macropterous,

Fig. 9.—*Catantopinae: a) Catantops melanosticus,* 1.5 mm.; *b) Leptysma marginicollis,* 1.3 mm.; *c) Podisma pedestris,* 1.1 mm.; *d) Cophopodisma costae* (not measured). Sclerites of sense organ: *e) Catantops melanostictus; f) Leptysma marginicollis; g) Paracardenius lineatus; h) Meridacris diabolica; i) Palniacris rugulosa. Cyrtacanthacridinae: j) Schistocerca gregaria,* 2.6 mm.; *k) Cyrtacanthacris tatarica,* 2.5 mm.

less frequently brachypterous; one species, *Bradynotes pinguis* Scudder, 1898, is apterous, and unusual in that apterous species with tympanal organs generally have membranes that are sclerotized, not transparent (Table 10).

The fourth group contains species with a poorly developed sclerotized membrane of roughly circular or irregular shape (e. g. *Cophopodisma costae* La Greca, 1955, fig. 9, *d*). There is no shell covering and frequently no subtympanal ridge. The majority of species are apterous, some are micropterous, one (*Taeniophora dentipes* Stål, 1873) is brachypterous and one (*Meltripata picta* I. Bolívar, 1923) macropterous. It is rare for species with large wings to have sclerotized tympanal membranes.

The fifth group contains species without a tympanal organ. This group is mainly represented by apterous species, but there are two exceptions: one (*Opiptacris signata* Willemse, 1935) is micropterous and the other (*Phalaca sarawakensis* Willemse, 1938) is an extremely rare case, being macropterous. Species with tegmina and no tympanal organ very rarely occur in *Acrididae,* unless these characters are normal for the whole group.

It is interesting to note that *Meltripata picta* with a small sclerotized membrane and *Phalaca sarawakensis* with no membrane are both macropterous and both from Sarawak. The brachypterous species *Taeniophoa dentipes* with a small sclerotized membrane is from Colombia.

From the above descriptions it appears that macropterous species more frequently have membranes which are more deeply depressed and shell coverings of varying degrees of development, while micropterous species mostly have no shell coverings or only small ones and membranes which are not depressed or are only slightly so. Apterous species generally have either a very reduced, sclerotized membrane or none at all. Approximately one-third of the genera have a shell covering and two-thirds have a subtympanal ridge. The subtympanal ridge is frequently absent and this is particularly noticeable in species without a definite lower margin of the membrane. Some species (e. g. *Leptysma marginicollis* Serville, 1839) have a wide area where there is no definite margin to the membrane. This character may occur with or without a shell covering. In some cases the membrane has no definite margin but a subtympanal ridge is present (as e. g. *Leptysma marginicollis,* fig. 9, *b*).

The sclerotic supports of the sensory structure are of the usual *Acri-*

TABLE 10.

Subfamily CATANTOPINAE.

Variation of the tympanal organ in relation to tegmen length and presence or absence of a sound-producing mechanism (+ present, — absent).

Tympanal Organ				Wing Development (Number of specimens studied)								Sound-producing mechanism
				Macropterous		Brachypterous		Micropterous		Apterous		
Membrane	Shell cover	Subtympanal lobe	Subtympanal ridge	♂	♀	♂	♀	♂	♀	♂	♀	
Transparent, moderately depressed	+	—	+ or —	42	49	1	3	4	5			None detected
Transparent, shallowly depressed	Small, or slight tendency only	—	+ or —	18	24	1	1	10	7			ditto
Transparent, level or almost level with body surface	—	—	+ or —	21	32	10	15	41	48	1	1	ditto
Sclerotized, poorly developed, irregular in shape	—	—	+ or –	1		1	1	5	6	10	10	ditto
Absent	—	—	—	1	1				1	15	17	ditto

didae type (as e. g. in *Catantops melanostictus,* fig. 9, *e*) but variations are found especially when the membrane is poorly developed. The styliform body may be very small (as in *Leptysma marginicollis,* fig. 9, *f*) or elongate (as in *Paracardenius lineatus* Uvarov, 1953, fig. 9, *g*); in *Palniacris rugulosa* Henry, 1940, (fig. 9, *i*) it is an expanded structure even larger than the folded body. In the sclerotized membrane of *Meridacris diabolica* Roberts, 1937 (fig. 9, *h*) the folded body is absent altogether; this is rare, as less variation is found in the folded body generally. The styliform body is often reduced or absent when the tympanal organ is very poorly developed, and in extreme cases there is often no trace of the sensory structure at all (as e. g. in *Cophopodisma costae,* fig. 9, *d*). The fusiform body and pyriform vesicle are found in all species without great variation except when the membranes are very poorly developed.

Generally the membrane is similar in the male and female of the same species, but in some micropterous forms the membrane is slightly more depressed at the posterior margin in the male than in the female, and may even possess a small shell covering in the male only (as in *Dinaria mirzayani* (Popov, 1950). In a few species there is a tendency towards a subtympanal lobe (e. g. in *Inusia chipmani* Bruner, 1906). The lobe never develops to a great extent, in this subfamily.

Definite stridulatory mechanisms are unknown.

Owing to the very large number of genera investigated in this subfamily, a list of their names is omitted.

Cyrtacanthacridinae.
(Fig. 9, *j-k;* Table 11).

A tympanal organ is present in all genera studied. The membrane is transparent, oval and depressed beneath the body surface at the posterior margin. The degree of depression varies considerably. The lower anterior margin of the membrane is raised slightly above the surface. There is no subtympanal lobe, but a subtympanal ridge may be present though not well developed. The sclerotic supports of the sensory structure are of the normal *Acrididae* type. The styliform body is smaller than in *Eyprepocnemidinae,* and the folded body, the fusiform body and the pyriform vesicle are clearly differentiated.

The species studied may be divided into groups according to the

TABLE 11.

Variation of the tympanal organ in relation to tegmen length and presence or absence of a sound-producing mechanism (+ present, — absent).

Subfamily	Tympanal Organ				Wing Development (Number of specimens studied)								Sound-producing mechanism
					Macropterous		Brachypterous		Micropterous		Apterous		
	Membrane	Shell cover	Subtympanal lobe	Subtympanal ridge	♂	♀	♂	♀	♂	♀	♂	♀	
Cyrtacanthacridinae	Transparent, deeply, depressed	+	—	weak	8	8							None detected
	Transparent, moderately depressed	slightor absent	—	weak	14	16							ditto
Egnatiinae	Transparent, moderately depressed	+	+	—	5	5							present

degree of depression of the membrane, but exact grouping is difficult, because intermediate forms occur.

The first group contains species with a deeply depressed membrane and a shell cover. The extent of the development of the shell cover varies, and in general the deeper the membrane the larger the cover. The deepest membrane and the largest shell covering are in *Schistocerca gregaria* (fig. 9, *i*). Genera and species belonging to the first group are: *Anacridium aegyptium* (Linnaeus, 1764), *Austracris guttulosa* (Walker, 1870), *Nomadacris septemfasciata* (Serville, 1838), *Ornithacris cyanea* (Stoll, 1813), *Orthacanthacris humilicrus* (Karsch, 1896), *Patanga succincta* (Linnaeus, 1763), *Rhadinacris schistocercoides* (Brancsik, 1893), *Schistocerca gregaria* (Forskål, 1775).

The second group contains species with the membrane only moderately depressed beneath the body surface (as e. g. in *Cyrtacanthacris tatarica,* fig. 9, *k*). The shell covering is poorly developed or absent.

Genera and species belonging to this group are: *Acanthacris ruficornis* (Fabricius, 1787), *Acridoderes crassus* I. Bolívar, 1889, *Adramita arabicum* Uvarov, 1930, *Bryophyma debilis* (Karsch, 1896), *Chondracris rosea* (De Geer, 1773), *Cristacridium uvarovi* Willemse, 1932, *Cyrtacanthacris tatarica* (Linnaeus, 1758), *Finotina radama* (Brancsik, 1893), *Gowdeya picta* Uvarov, 1923, *Kraussaria angulifera* (Krauss, 1877), *Melicodes graminae* (Stoll, 1877), *Pachyacris violascens* (Walker, 1870), *Pachynotacris amethystina* (I. Bolívar, 1908). *Phyxacra strenua* (Walker, 1870), *Rhytidacris tectifera* (Karsch, 1896), *Valanga irregularis* (Walker, 1870).

All species of this subfamily studied are macropterous. No sound-producing mechanism is known.

Egnatiinae.

(Table 11).

A tympanal organ is present in all genera studied, and is uniform in structure throughout the subfamily. The membrane is transparent, oval, and depressed at the posterior margin. A small shell covering and a small lobe are present. The sclerotic supports of the sensory structure are of the usual *Acrididae* type; the styliform body is thin and elongate.

A stridulatory mechanism is present in most genera. All the species studied are macropterous.

Species examined are: *Egnatius apicalis* (Stål, 1876), *Leptoscirtus isphahanicus* Uvarov, 1932, *Charora crassivenosa* Saussure, 1888, *Egnatiella major* I. Bolívar, 1914, *Egnatioides coerulans* (Krauss, 1893).

Acridinae.

(Fig. 10, *a-g;* Table 12).

A tympanal organ is usually present but occasionally absent. The membrane is oval, transparent and depressed beneath the body surface at the posterior margin. The degree of depression varies considerably. A shell-like covering is present and may be very reduced or very large. There is usually a subtympanal lobe or ridge. The sclerotic supports of the sensory structure are of the usual *Acrididae* type, but variation occurs in the styliform body, which may be long and very thin, long and splayed out dorsally (in which case it is a large structure) or small, circular and difficult to detect. In a few species the pyriform vesicle is relatively large. There is no great variation in the folded body or the fusiform body.

The species may be divided into groups according to the characters of the tympanal organ, but exact grouping is sometimes difficult because of intermediate forms. Species with a subtympanal lobe always have a shell covering, but a covering is also present in some species which lack a lobe.

The first group has a deeply depressed membrane, a large shell covering and generally a small to moderate-sized subtympanal lobe. The largest shell covering in the subfamily is found in *Locustana pardalina* (Walker, 1870) (fig. 10, *a*). The largest subtympanal lobe in the subfamily is found in *Locusta migratoria* (Linnaeus, 1785) (fig. 10, *b);* this is unusual in being approximately triangular rather than semicircular. All genera in this group are macropterous.

The second group contains most of the genera of the subfamily. The membrane is not so deeply depressed as in the first group, and the shell covering is only moderately developed. *Acteana alazonica* Karsch, 1896 (fig. 10, *c*) is unusual in that it possesses a large shell covering and only a subtympanal ridge, not a lobe. In general, the subtympanal lobe is small to moderate-sized (as e. g. in *Acrotylus insubricus* (Scopoli,

1786) (fig. 10, *d*), or absent altogether, only a ridge being present. In some genera the males and females show slight differences in structure, the males having deeper-set membranes and slightly larger shell coverings. Structural differences between the sexes are not of frequent occurrence but were observed in *Chokwea burri* Uvarov, 1953 (fig. 10,

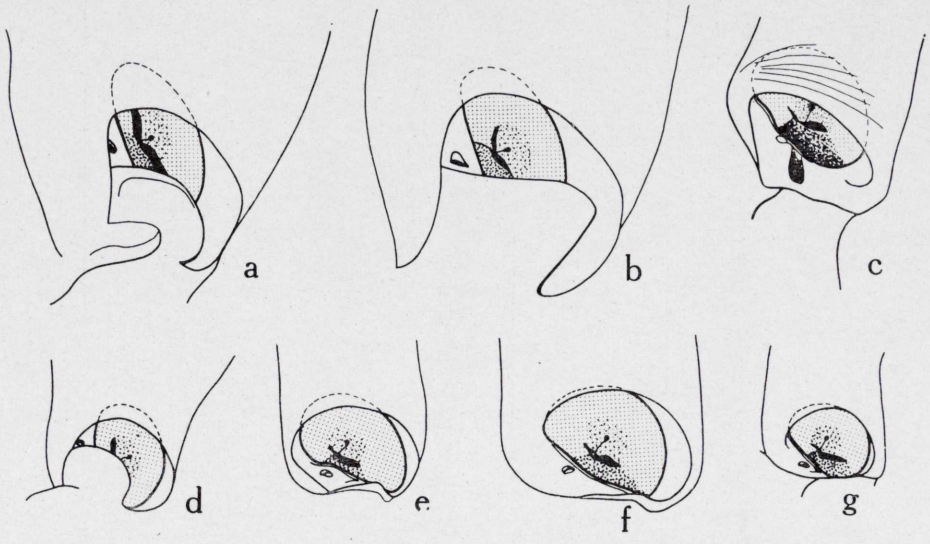


Fig. 10.—*Acridinae: a) Locustana pardalina,* 2.4 mm.; *b) Locusta migratoria,* 2.4 mm.; *c) Acteana alazonica,* 0.9 mm.; *d) Acrotylus insubricus,* 1.4 mm.; *e) Chokwea burri* — ♂, 1.4 mm.; *f) Ch. burri,* ♀, 1.5 mm.; *g) Pseudophlaeoba henryi,* 1.0 mm.

e, f), *Lobopoma ambages* Karsch, 1896, *Weenenia thomasseti* Miller, 1932, *Psophus stridulus* (Linnaeus, 1758), *Chimarocephala pacifica* (Thomas, 1873), *Orthochtha dasycnemis* (Gerstaecker, 1896) and *Metaleptea brevicornis* (Linnaeus, 1764). The females of these species are border cases between this group and the next owing to their membranes being less depressed.

Species studied with subtympanal lobes are mainly macropterous, but a few are brachypterous. Those with a subtympanal ridge are macropterous, brachypterous or micropterous.

A third group have a very shallowly depressed membrane; the shell covering and subtympanal lobe are poorly developed, or the lobe is absent and a ridge present. *Pseudophlaeoba henryi* I. Bolívar, 1914 (fig. 10, *g*) is in this group. The species are macropterous, brachypterous or micropterous.

TABLE 12.

Subfamily ACRIDINAE.

Variation of the tympanal organ in relation to tegmen length and presence or absence of a sound-producing mechanism (+ present, — absent).

Tympanal Organ				Wing Development (Number of specimens studied)								Sound-producing mechanism
				Macropterous		Brachypterous		Micropterous		Apterous		
Membrane	Shell cover	Subtympanal lobe	Subtympanal ridge	♂	♀	♂	♀	♂	♀	♂	♀	
Transparent, deeply, depressed	+	+	—	9	9							Often present
Transparent, moderately depressed	+ +	+ —	— +	84 26	81 26	1	3 2	6	6			ditto
Transparent, shallowly depressed	poor poor	poor —	— +	5 5	5 4	1	2	1 7	1 7			ditto
Absent	—	—	—					1	1	1	1	None detected

Judging from the species studied in these groups, approximately one-third of the genera in this subfamily possess a subtympanal ridge and two-thirds a subtympanal lobe. Micropterous species do not usually have a lobe. No species were found with sclerotized or very poorly developed membranes but two, *Rashidia perplexa* Uvarov, 1932 and *Dysanema malloryi* Uvarov, 1925 have no tympanal organs at all. The former has very poorly developed tegmina, the latter is apterous. Winged species, even those in which the wings are poorly developed, usually have a tympanal organ. *Rashidia* therefore appears unique in the subfamily in this respect.

Sound-producing mechanisms are known to be present in many genera but most of the genera are insufficiently studied in this respect.

EREMOGRYLLINAE.

(Table 13).

Two genera and species were studied, *Notopleura rothschildi* Uvarov, 1923 and *Eremogryllus hammadae* Krauss, 1902. Both have tympanal organs, which are similar in the both sexes. The membrane is oval, transparent and depressed beneath the body surface; a moderately developed shell covering and a reduced subtympanal lobe are present. The sensory structure is of the usual *Acrididae* type. The folded body is relatively large, while the styliform body is thin and elongate. The pyriform vesicle is small, and the fusiform body visible.

Both genera are macropterous. A sound-producing mechanism is present.

TRUXALINAE.

(Fig. 11, *a-h;* Table 13).

A tympanal organ is present and well developed in all species studied, showing no signs of regression. The membrane is transparent, never sclerotized, and is usually moderately depressed beneath the body surface; the degree of depression varies from deep to shallow. The most striking character is the shell covering which is generally quite large and in a few genera show an extreme degree of development. The ventral margin of the membrane is clearly defined. A much reduced subtympanal lobe or a ridge is present. The sensory structure

TABLE 13.

Variation of the tympanal organ in relation to tegmen length and presence or absence of a sound-producing mechanism (+ present, — absent).

Subfamily	Tympanal Organ				Wing Development (Number of specimens studied)								Sound-producing mechanism
					Macropterous		Brachypterous		Micropterous		Apterous		
	Membrane	Shell cover	Subtympanal lobe	Subtympanal ridge	♂	♀	♂	♀	♂	♀	♂	♀	
Eremogryllinae	Transparent, depressed	+	+	—	2	2							Present
Truxalinae	Transparent, moderately depressed	Very large	+	—	5	5							ditto
	ditto	Moderate	+	—	27	25	2	3					ditto
	ditto	ditto	—	+	36	33	8	7	2	6			ditto
	Transparent, shallowly depressed	Small	—	+	2	2	3	2		1			ditto

is of the usual *Acrididae* type and fairly uniform, but the styliform body varies.

A grading of characters is evident but an attempt was nevertheless made to group the species studied in accordance with the most distinctive combinations of characters of the tympanal organ.

The species of the first group are separated from the rest of the *Truxalinae* by the exceptionally large shell covering, which has developed to such an extent that most of the membrane is covered and the sensory structure is not seen at all. There is also a very small subtympanal lobe, and the two structures together practically cover the membrane (as e. g. in *Stenobothrus rubicundus,* fig. 11, *a*). The membrane in these species is moderately depressed. All are macropterous.

The species studied in this group are: *Chorthippus brunneus* (Thunberg, 1815), *Gomphocerippus rufus* (Linnaeus, 1758), *Myrmeleotettix maculatus* (Thunberg, 1815), *Omocestus viridulus* (Linnaeus, 1758), *Stenobothrus rubicundus* (Germar, 1817).

The second group has a well developed shell covering, but the sensory structure is partly or completely visible (as e. g. in *Pnorisa squalus capensis,* Walker, 1870, fig. 11, *b*). The membrane is moderately depressed, the deepest being in *Truxaloides braziliensis* (Drury, 1773), fig. 11, *f*) and *Chromotruxalis crocea* (I. Bolívar, 1889). Either a small subtympanal lobe or a ridge is present. The majority of species in this group are macropterous, but a few are brachypterous or micropterous.

The third group has only a small shell covering and the membrane is only shallowly depressed. A subtympanal ridge is present, but no lobe. These species are macropterous, brachypterous or micropterous and include: *Brainia hirsuta* Uvarov, 1922, *Morseiella flaviventris* Bruner, 1925, *Primnia sanctaehelenae* (Stål, 1861), *Pseudegnatius reyneckei* Dirsh, 1956, *Tinaria viridipes* Walker, 1875 and *Mermiria neomexicana* (Thomas, 1870) (fig. 11, *c*).

Among the 85 genera of this subfamily which were studied, 51 possess a subtympanal ridge (the most weakly developed being that of *Cophohippus burri* Uvarov, 1953) and 34 have a subtympanal lobe; but the lobe is never well developed and in many cases it is difficult to decide whether to grade the structure as a lobe or as a ridge. The largest lobes in the subfamily do not cover the sensory structures; they are found in the genera *Truxaloides, Chromotruxalis, Gomphocerippus* and *Stenobothrus.*

The size and shape of the aperture between the edge of the shell

covering and the edge of the membrane or of the subtympanal lobe varies considerably. The aperture of *Truxaloides braziliensis* is very wide, while that of *Stenobothrus rubicundus* is narrow and elongate.

Fig. 11.—*Truxalinae: a) Stenobothrus rubicundus,* 1.5 mm.; *b) Pnorisa squalus capensis,* 1.3 mm.; *c) Mermiria neomexicana,* 1.7 mm.; *d) Arcyptera fusca,* ♀; 2.6 mm.; *e) A. fusca* ♂, 2.2 mm.; *f) Truxaloides braziliensis,* 2.2 mm. Sclerites of the sense organ: *g) Cophohippus burri; h) Mesopsis gracilicornis.*

The styliform body varies in form from thin and elongate (e. g. that of *Mesopsis gracilicornis* (Krauss, 1877), (fig. 11, *h*) to small and circular or even splayed out (e. g. *Cophohippus burri,* fig. 11, *g*).

In this subfamily more examples of sexual dimorphism in the tympanal organ were found than in other subfamilies of *Acrididae,* but these are not numerous and generally the males and females of the same species have identical tympanal organs, except in size. Where dimorphism occurs the male often has a slightly more depressed membrane than the female. This may be difficult to detect unless the specimens are placed side by side under the microscope and compared. Sexual dimorphism occurs in: *Syrbula admirabilis* (Ulmer, 1864), *Arcyptera fusca* (Pallas, 1773) (fig. 11, *d, e*), *Sinipta dalmani* Stål, 1860 and *Dichromorpha australis* Bruner, 1900.

The majority of species are macropterous. No wholly apterous species have been studied. A sound-producing mechanism is always present.

Degree of correlation between occurence of sound-producing mechanisms and of tympanal organs in "Acridomorpha".

In *Acridomorpha* some families have both a sound-producing mechanism and a tympanal organ. Others, however, have a sound-producing mechanism but no tympanal organ (e. g. *Tanaoceridae, Pneumoridae, Xyronotidae),* while others again have a tympanal organ but do not appear to possess any sound-producing mechanism. There are also families (e. g. *Eumastacidae, Trigonopterygidae)* which have neither tympanal organ nor sound-producing mechanism, so far as is known.

However, observations on living specimens have confirmed that various types of sound-producing mechanism exist that cannot be detected on dried specimens. Uvarov (1966) gives some of the main types of sound-production in addition to stridulation: namely, wing crepitation, flight noise, wing beat, mandibular noise, drumming of the tarsi, abdomen or tegmina against the ground, and hissing of liquid expelled from the spiracles. The writer has also heard noise produced by specimens of *Proscopiidae* which are apterous, have no tympanal organ and do not appear to have any special sound-producing mechanism; when they were disturbed, high pitched squeaks were heard, but it was impossible to say how the noise was produced. Another observation

was made on a female *Hoplolopha* sp. (Family *Pamphagidae).* This specimen also was apterous, and it had a sclerotized tympanal membrane. It produced sound by rubbing the hind tibia on its irregularly rough spiny abdomen. Until this had been observed it was thought that females of this species did not produce sound as no specialised structures had been found. Another specimen which produced a sound in the laboratory was a female *Sphodromerus* sp.; this was achieved while the insect was stationary, by rapid vibration of the outspread wings and tegmina.

It appears then that many species produce sound even though the tympanal organ is absent, and it is to be assumed, pending much more investigation, that many species not at present known to produce sound can in fact do so.

From the information and material available to date it appears that in *Acridomorpha* the tympanal organ is characteristically absent in eight families, *Eumastacidae, Proscopiidae, Pneumoridae, Tanaoceridae, Xyronotidae, Trigonopterygidae, Lathiceridae* and *Lentulidae,* and also in the subfamily *Lithidiinae* of *Acrididae.* Among these, highly developed stridulatory mechanisms are present in *Tanaoceridae, Pneumoridae* and *Xyronotidae.*

In six families which have a tympanal organ, *Charilaidae, Pamphagidae, Pyrgomorphidae, Ommexechidae, Pauliniidae* and *Acrididae,* a sound-producing mechanism is known in *Charilaidae, Pamphagidae* and *Acrididae.* In the largest family, *Acrididae,* a tympanal organ is generally present in all of the 17 subfamilies except *Lithidiinae,* but stridulatory mechanisms or other sound-producing devices are detected in only 9 subfamilies: *Dericorythinae, Romaleinae, Hemiacridinae, Calliptaminae, Eyprepocnemidinae, Egnatiinae, Acridinae, Eremogryllinae* and *Truxalinae.* Information regarding sound production in the other subfamilies, *Chilacridinae, Tropidopolinae, Oxyinae, Coptacridinae, Euryphyminae, Catantopinae* and *Cyrtacanthacridinae,* is at present lacking, but it may well occur by means not yet detected.

Relation between the body size index and the diameter of the tympanal membrane.

The tympanal index, representing the diameter of the membrane in terms of the body index, was calculated for each specimen studied.

The method of measuring and calculating the tympanal index is explained at the beginning of this work.

Scatter diagrams (figs. 12-20; table 14) were first prepared, with the

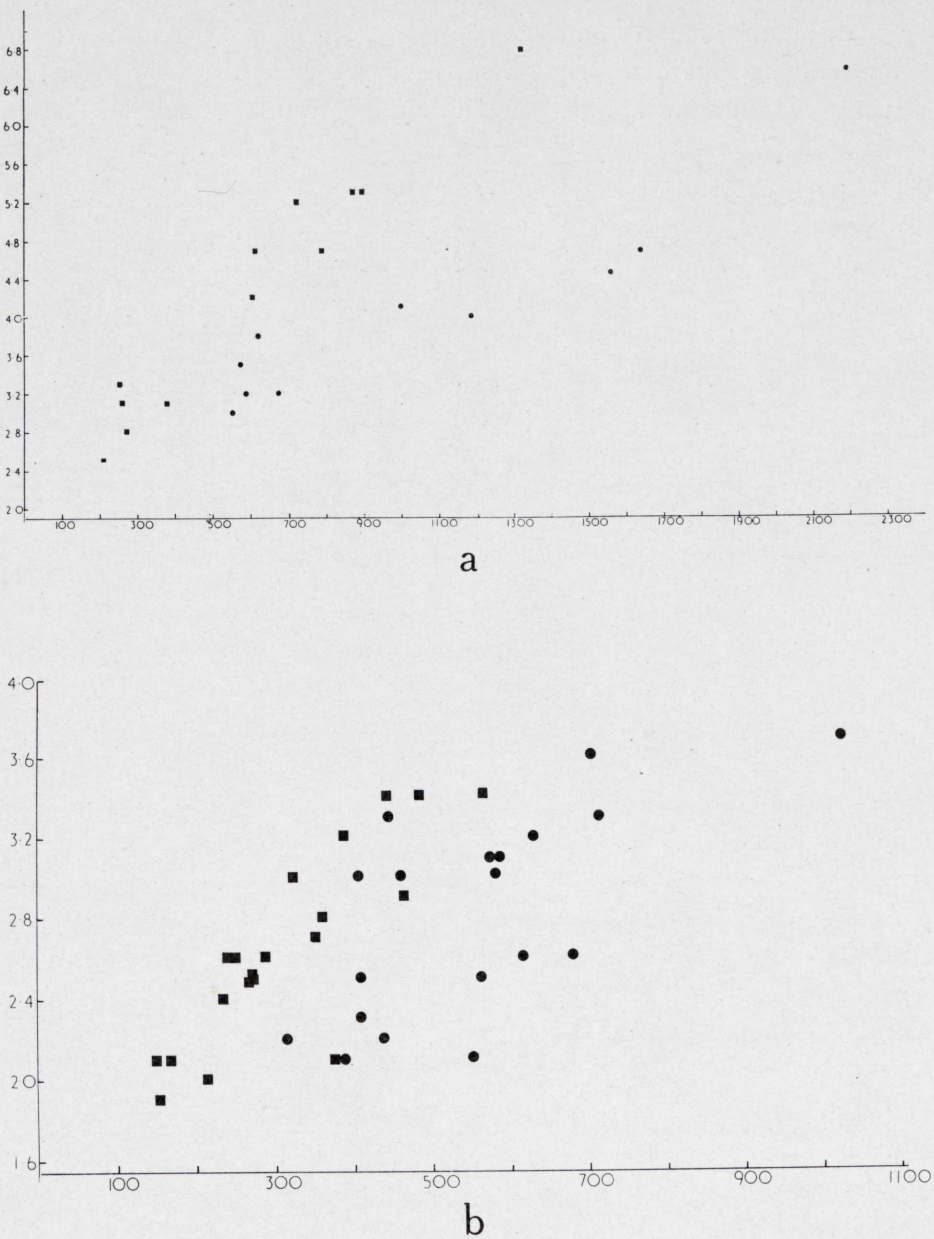


Fig. 12.—*a) Porthetinae.* Scatter diagram: square — male, round — female; ordinate, diameter of tympanal membrane; abscissa, body size index. *b) Akicerinae.* Scatter diagram: square — male, round — female.

diameter of the membrane in mm as ordinate and the body size (L × W in mm) as abscissa. Males and females were indicated with separate symbols. Each main subfamily of *Pamphagidae* and *Acrididae* was dealt with separately, and the family *Pyrgomorphidae* as a whole was also included.

In all the families and subfamilies of *Acridomorpha* it was found that although the males have a smaller body size than the females, the diameter of the membrane is relatively larger in the males. The general shape of the body varies greatly, that is, some species are long and narrow, as in *Mesopsis gracilicornis* Krauss, 1877 (subfamily *Truxalinae),* body length: ♂ 55.5 mm, ♀ 62.0 mm, body width: ♂ 2.9 mm, ♀ 3.3 mm, L × W = ♂ 160.95, ♀ 204.60; while others are short and broad, e. g. *Trachyptrella anderssonii* Stål, 1875 (family *Pamphagidae),* body length: ♂ 47.1 mm, ♀ 75.1 mm, body width: ♂ 18.5 mm, ♀ 29.6 mm, L × W = ♂ 871.35, ♀ 2222.96. The membranes of both these species are transparent and appear well developed. The diameters of the membranes measure: *M. gracilicornis* ♂ 1.5 mm, ♀ 1.6 mm, *T. anderssonii* ♂ 5.3 mm, ♀ 6.4 mm. Thus, $\frac{D}{L \times W}$ in *M. gracilicornis* is ♂ 0.00932, ♀ 0.00782, in *T. anderssonii* ♂ 0.00608, ♀ 0.000288. The tympanal index is therefore, in *M. gracilicornis* ♂ 9.32, ♀ 7.82, and in *T. anderssonii* ♂ 6.08, ♀ 2.88. In this particular example, the larger species *T. anderssonii* has the smaller tympanal index. From general observation and examination it is impossible without measurements and calculations to state which species has the larger membrane in relation to its body size. Scatter diagrams illustrate each subfamily in this respect. These two species just considered are from different families, but it is found that within each family and subfamily the size of the membrane in both sexes has a general tendency to increase with the body size though the rate of increase is characteristically different in each of the families and subfamilies (scatter diagrams, figs. 12-20).

In *Porthetinae,* one of the subfamilies of *Pamphagidae,* the majority of males are macropterous with a good sound-producing mechanism, and the tympanal membrane is transparent, while the females are all apterous (except *Trachypetrella)* with reduced, sclerotized tympanal membrane. As can be seen from the scatter diagrams (fig. 12, *a*) the difference between the sexes in the size of the body and that of the

tympanal membrane is quite distinct, the female having a small membrane and a larger body size.

The subfamily *Akicerinae* (fig. 12, *b*) is a fairly compact group. Its genera are mostly macropterous in both sexes and have a smaller range of body size than *Porthetinae* or *Pamphaginae*.

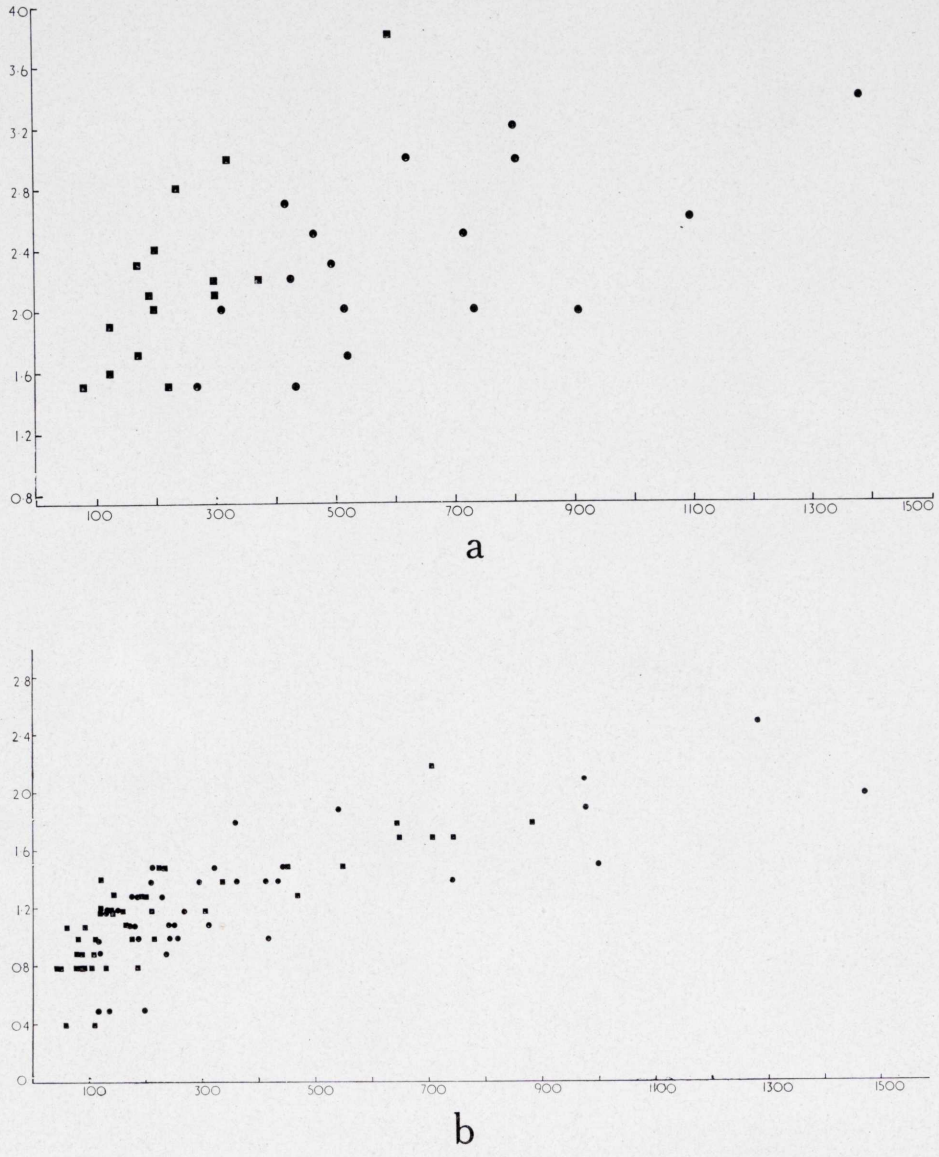


Fig. 13.—*a) Pamphaginae.* Scatter diagram: square — male, round — female; ordinate, diameter of tympanal membrane; abscissa, body size index. *b) Pyrgomorphidae.* Scatter diagram: square — male, round — female.

The *Pamphaginae* have a larger body-size range than the *Akicerinae* but a smaller one than *Porthetinae*. The males form a compact

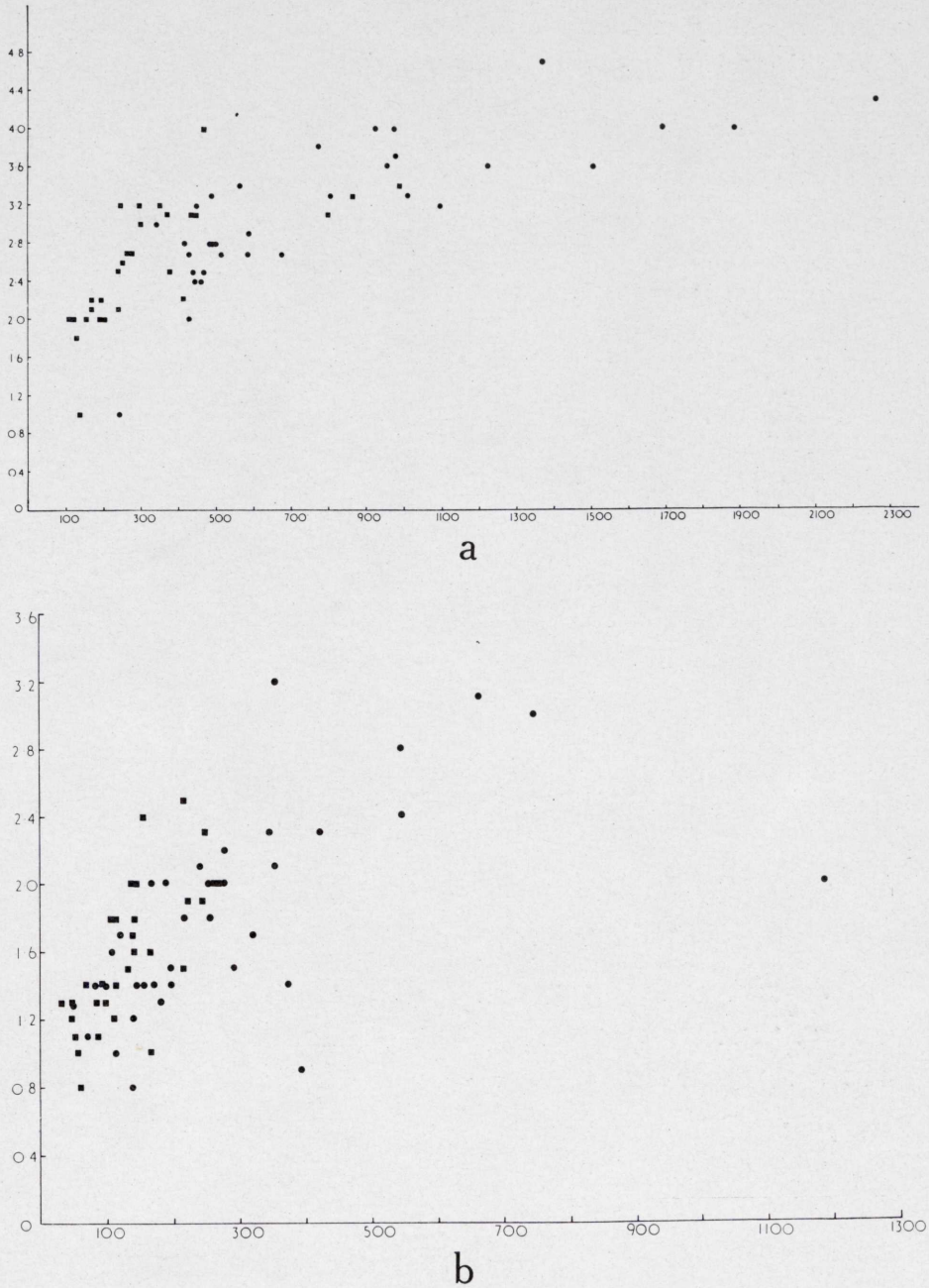


Fig. 14.—*a) Romaleinae.* Scatter diagram: square — male, round — female; ordinate, diameter of tympanal membrane; abscissa body size index. *b) Hemiacridinae.* Scatter diagram: square — male, round — female.

group while the females are spread loosely (fig. 13, *a*). The variability in correlation between the body size index and membrane size is more than in any other *Acridomorpha*. This may be due to some of the membranes being sclerotized and degenerate; or the subfamily may be heterogenous. All species are micropterous, or apterous.

The family *Pyrgomorphidae* shows a very large range of body size. The membrane is small in comparison to the rest of the superfamily *Acridoidea*. In the diagram (fig. 13, *b*) the males and females are intermingled. This may be due to the family being heterogeneous or to the membrane being less developed or more degenerate than in other *Acridoidea*. As many of the *Pyrgomorphidae* do not possess a membrane at all and a few are sclerotized it is assumed that this family is less specialised in this respect. Approximately half the specimens with a tympanal organ are macropterous and half are micropterous.

Each subfamily of the *Acrididae,* except the small ones *(Derycorythinae, Chilacridinae, Egnatiinae, Eremerogryllinae),* has been represented separately (figs. 14-20).

The subfamily *Romaleinae* (fig. 14, *a*) has a large range of body size. The membrane and the body size are generally both large. The range of body size is approximately that of *Porthetinae* but the male membranes in *Romaleinae* are relatively smaller. The sound-producing mechanism differs in these two subfamilies, being serrated veins on the wing of *Romaleinae* and specialised veins on the tegmen of *Porthetinae*. Both mechanisms are well developed.

The scatter diagram (fig. 14, *b*), of *Hemiacridinae* has a fairly compact distribution, except for three female specimens. This subfamily generally has a well developed sound-producing mechanism with thikkened transverse veinlets on the tegmen.

The *Tropidopolinae* (fig. 15, *a*) have a small body range. Membranes are present in all specimens studied. The distribution is fairly even, and the membranes are moderately large.

The *Oxyinae* (fig. 15, *b*) are a very compact group with the smallest body range.

The *Coptacridinae* (fig. 16, *a*) have a small body-size range. The membrane range is slightly larger than *Oxyinae*. As in *Oxyinae* stridulatory mechanisms are not known.

The *Calliptaminae* (fig. 16, *b*) have a moderate body range.

The *Euryphyminae* (fig. 17, *a*) have a small body-size range. The majority of specimens are macropterous, but there is no known stridu-

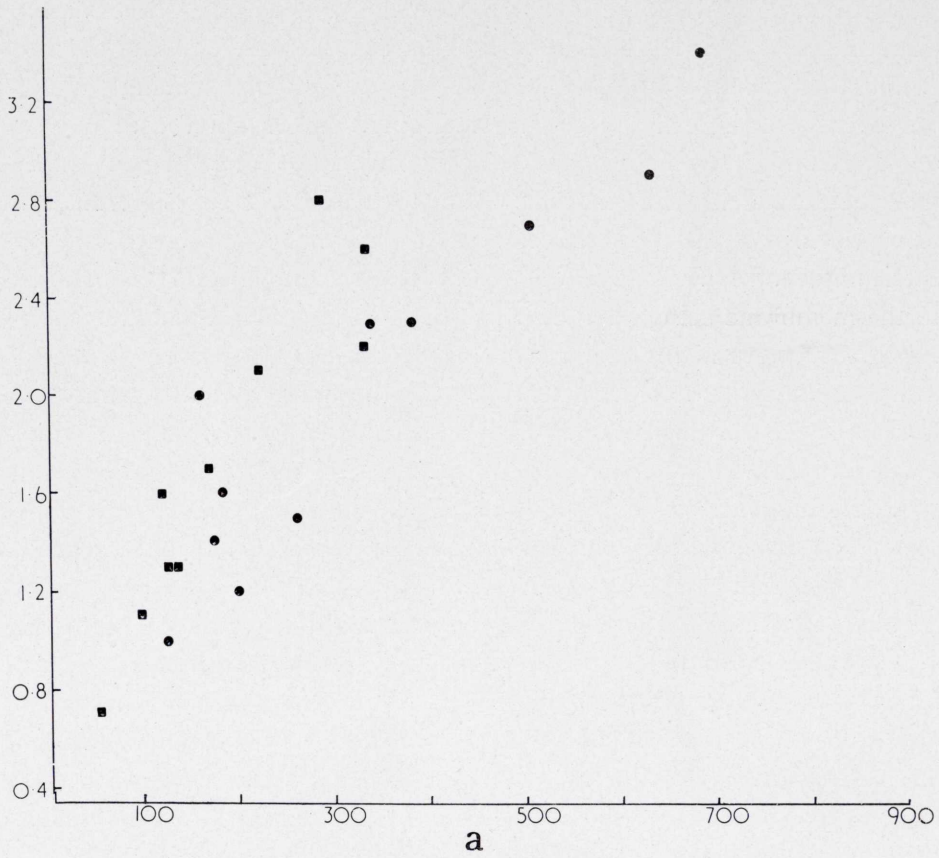


Fig. 15.—*a) Tropidopolinae.* Scatter diagram: square — male, round — female; ordinate, diameter of tympanal membrane; abscissa, body size index. *b) Oxyinae.* Scatter diagram: square — male, round — female.

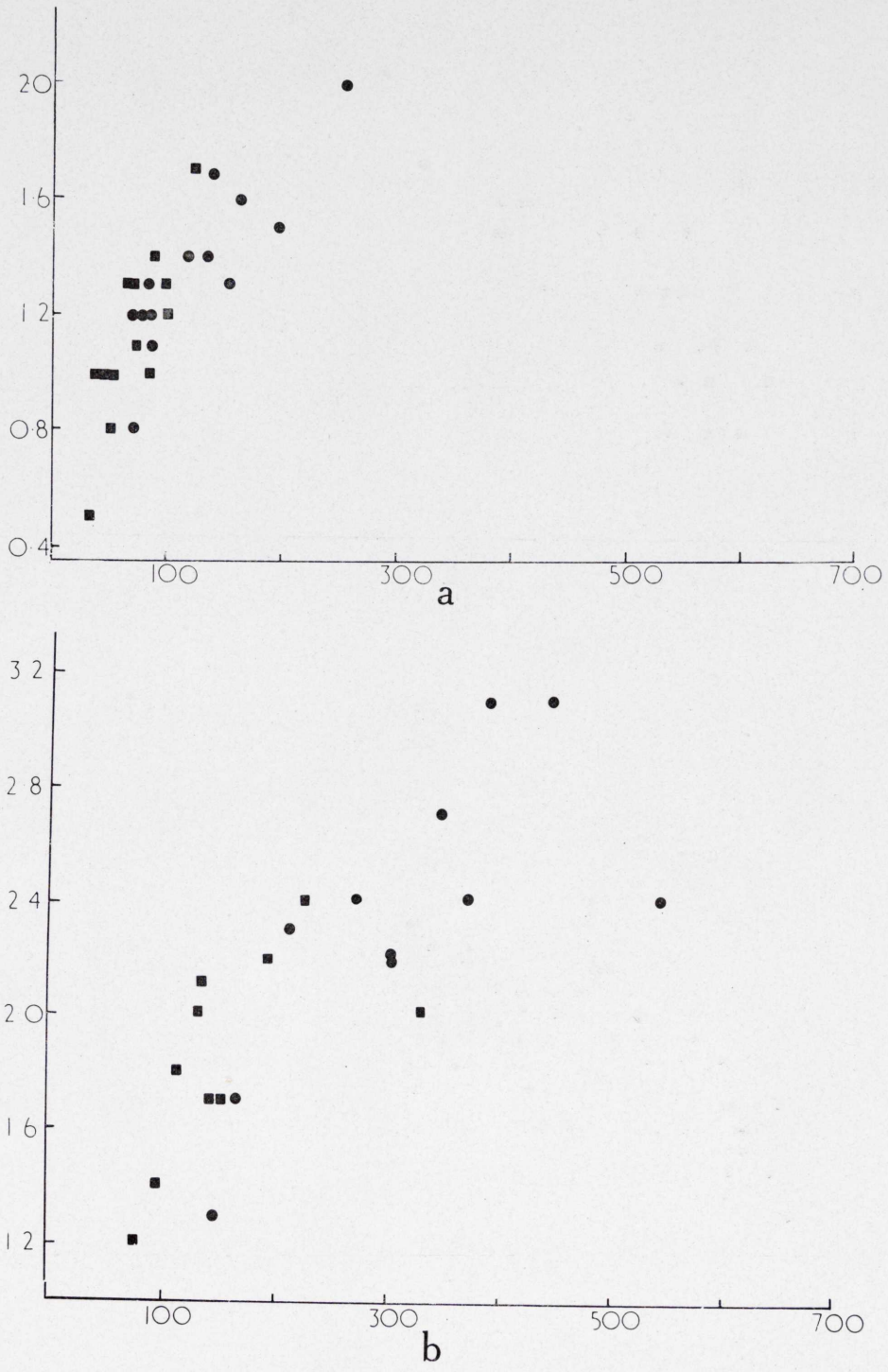
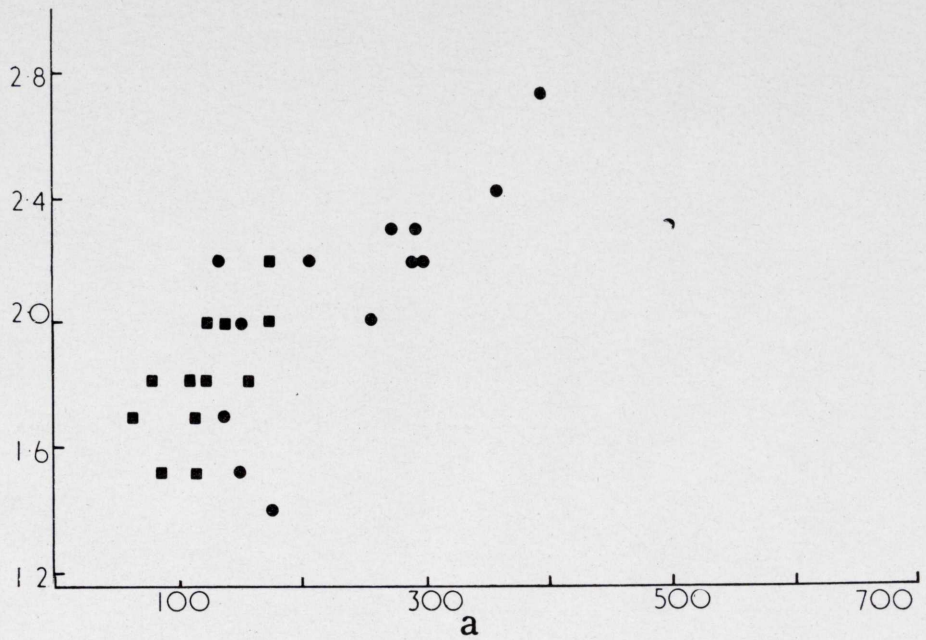


Fig. 16.—*a) Coptacridinae.* Scatter diagram: square — male, round — female; ordinate, diameter of tympanal membrane; abscissa, body size index. *b) Calliptaminae.* Scatter diagram: square — male, round — female.



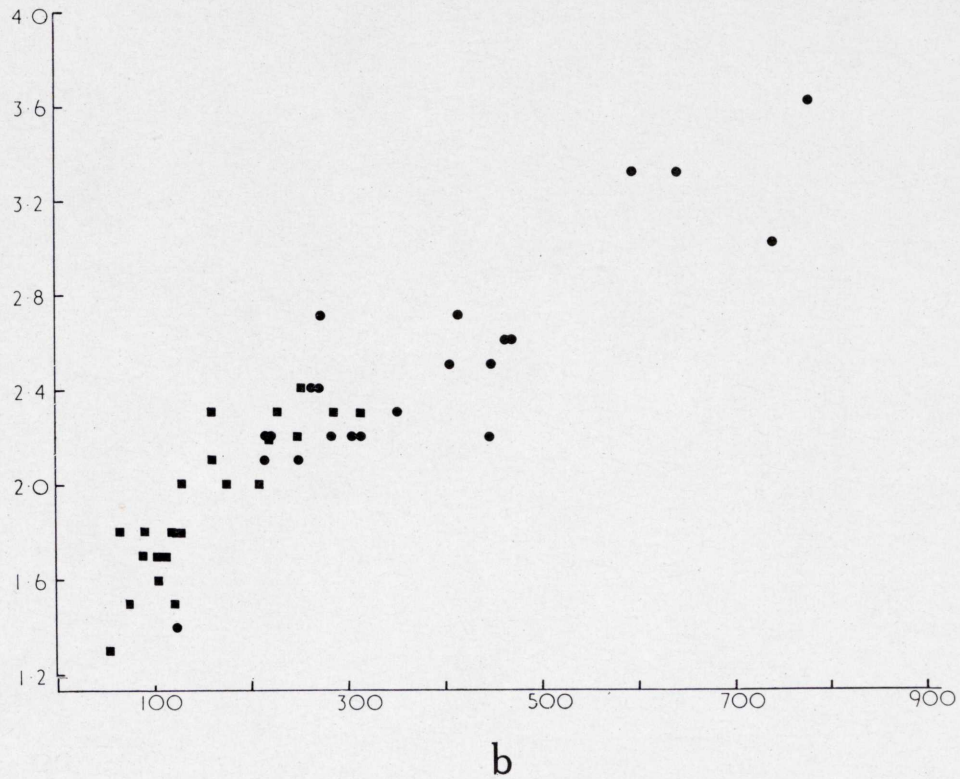


Fig. 17.—*a) Euryphyminae.* Scatter diagram: square — male, round — female; ordinate, diameter of tympanal membrane; abscissa, body size index. *b) Eyprepocnemidinae.* Scatter diagram: square — male, round — female.

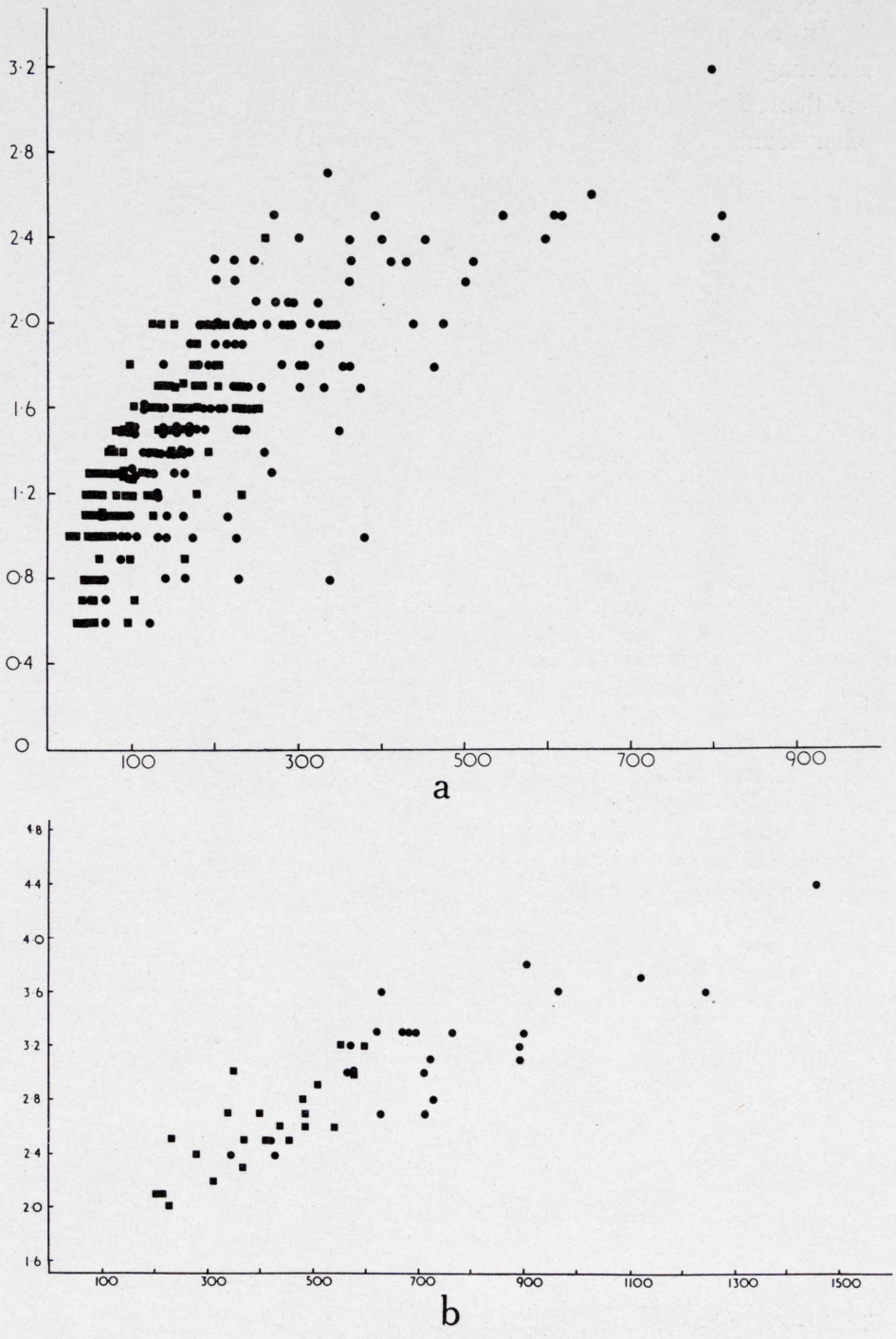


Fig. 18.—*a) Catantopinae.* Scatter diagram: square — male, round — female; ordinate, diameter of tympanal membrane; abscissa, body size index. *b) Cyrtacanthacridinae.* Scatter diagram: square — male, round — female.

latory mechanism. The membrane range is larger than *Coptacridinae* or *Oxyinae*.

In the *Eyprepocnemidinae* (fig. 17, *b*) the males have a smaller body size range than the females. The body and membrane ranges are larger than *Euryphyminae*. Stridulatory mechanisms are unknown, but other sound-producing mechanisms are sometimes present.

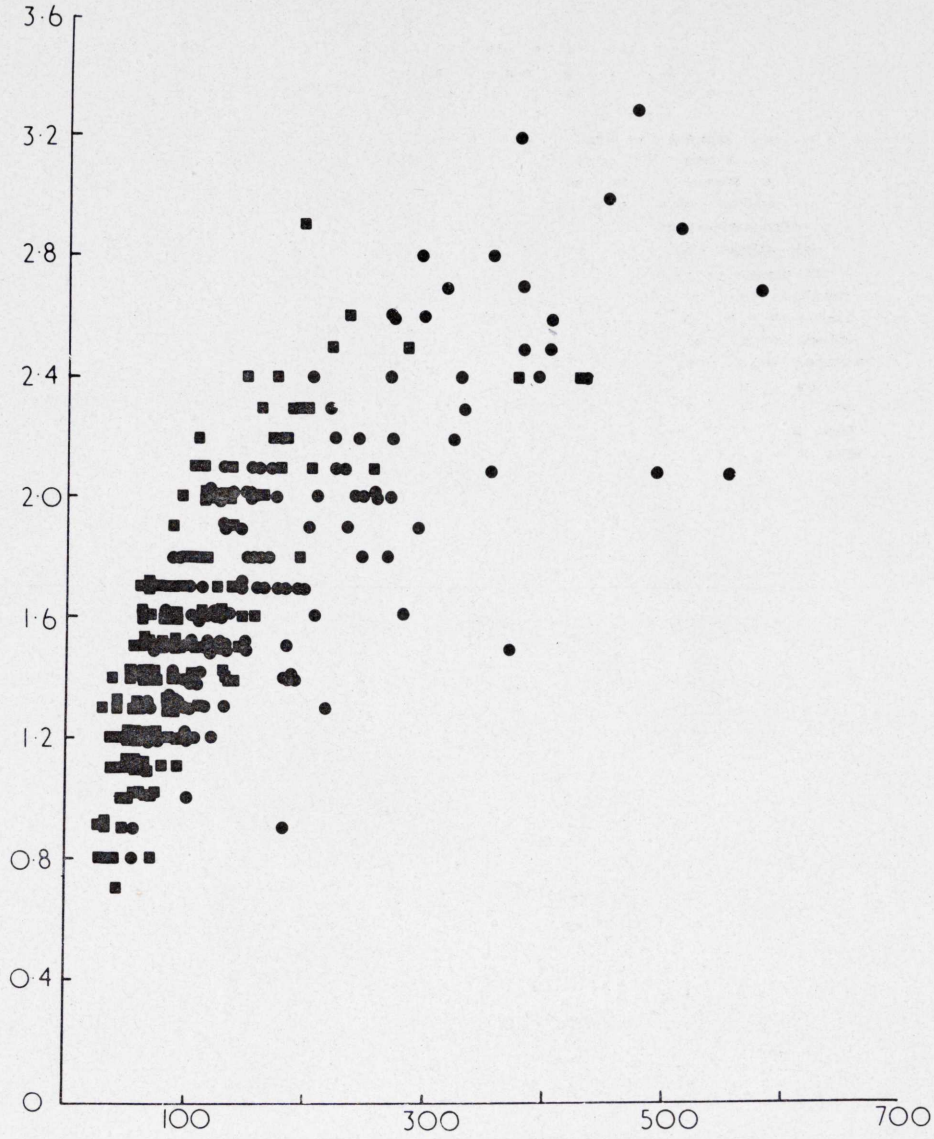


Fig. 19.—*Acridinae*. Scatter diagram: square — male, round — female; ordinate, diameter of tympanal membrane; abscissa, body size index.

The large subfamily *Catantopinae* (fig. 18, *a*) with no known stridulatory mechanism has a large range of body size; the diagram shows that the body range and membrane range are much smaller generally in the males than in the females.

The *Cyrtacanthacridinae* (fig. 18, *b*) have an even distribution.

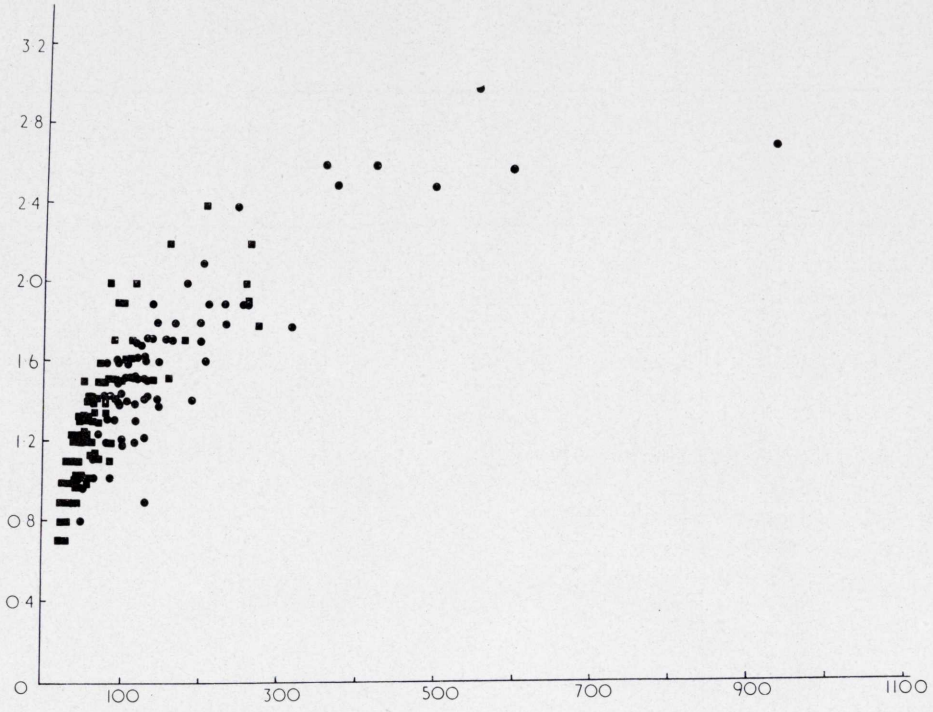


Fig. 20.—*Truxalinae.* Scatter diagram: square — male, round — female; ordinate, diameter of tympanal membrane; abscissa, body size index.

Although the body size and range are larger than *Truxalinae,* the membrane is smaller. No stridulatory mechanism is found.

The subfamily *Acridinae* (fig. 19) has a small body size index and large membrane range, showing a larger rate of increase of the membrane size. The group is not so compact as in *Truxalinae.* Sound-producing mechanisms of various types are mostly present.

The subfamily *Truxalinae* (fig. 20) with a well developed sound-producing mechanism has a large body size range but most of the spe-

cimens are small. If compared with the *Cyrtacanthacridinae* (fig. 18, *b*) the regression line of *Truxalinae,* i. e. the rate of increase of the membrane size, is seen to be much steeper indicating that the membrane is relatively much larger in *Truxalinae* for the body size.

TABLE 14.

Range of Body Size and Membrane Diameter.

Families and subfamilies	Body size (L × W)		Membrane diameter	
	♂♂	♀♀	♂♂	♀♀
Pamphagidae:				
Porthetinae	213.5 -1326.55	552.97-2222.96	2.5-6.8	3.0-6.4
Akicerinae	132.55- 569.85	315.62-1023.04	1.9-3.4	2.1-3.7
Pamphaginae ...	84.00- 581.49	274.55-1390.60	1.5-3.8	1.5-3.4
Pygomorphidae ...	40.04- 746.75	113.59-1471.26	0.4-2.2	0.5-2.5
Acrididae:				
Romaleinae	114.00- 993.85	242.52-2274.09	1.0-4.0	1.0-4.7
Hemiacridinae ...	31.50- 272.70	48.84-1184.4	0.8-2.5	0.9-3.2
Tropidopolinae ...	57.84- 335.34	100.16- 687.75	0.7-2.8	1.0-3.4
Oxyinae	37.80- 106.08	69.81- 200.20	1.0-1.6	1.0-1.8
Coptacridinae ...	36.80- 123.2	68.46- 256.80	0.5-1.7	0.8-2.0
Calliptaminae	77.40- 333.06	147.01- 547.80	1.2-2.4	1.3-3.1
Euryphyminae	65.32- 175.00	136.01- 501.84	1.5-2.2	1.4-2.7
Eyprepocnemidinae	66.50- 284.90	123.36- 782.40	1.3-2.4	1.4-3.6
Catantopinae	38.10- 263.72	43.75- 810.66	0.6-2.4	0.6-3.2
Cyrtacanthacridinae	228.47- 595.99	342.95-1458.85	2.0-3.2	2.4-4.4
Acridinae	43.60- 429.58	53.34- 585.80	0.7-2.9	0.8-3.3
Truxalinae	20.70- 273.45	36.00- 936.00	0.7-2.4	0.8-3.0

(Small families and subfamilies with only one or two genera studied are not included.)

THE TYMPANAL INDEX.

For each main subfamily of *Pamphagidae* and of *Acrididae,* and also for the families *Pamphagidae* and *Pyrgomorphidae* as such, calculations were made of the tympanal indices involving the mean, stan-

TABLE 15.

Mean of tympanal index of the sexes in families and subfamilies.

Families and subfamilies	Mean and Standard Error		Standard deviation		Difference between means ♂ - ♀	t	P
	♂	♀	♂	♀			
**Charilaidae*	15.87	8.35					
Pamphagidae:	9.44 ± 0.43	4.67 ± 0.04	2.99	1.33	4.77	10.15	< 0.001
Porthetinae	8.66 ± 0.89	4.49 ± 0.30	3.08	0.96	4.17	4.11	< 0.001
Akicerinae	9.10 ± 0.15	5.32 ± 0.07	0.68	1.15	3.78	12.55	< 0.001
Pamphaginae	10.55 ± 1.15	4.08 ± 0.32	4.48	1.33	6.47	5.74	< 0.001
**Ommexechidae*	17.88	9.49					
Pyrgomorphidae	8.02 ± 0.62	4.62 ± 0.36	4.40	2.26	3.40	4.37	< 0.001
**Pauliniidae*	16.4	10.5					
Acrididae:							
**Derycorythinae*	13.39	6.11					
**Chilacridinae*	8.01	4.35					
Romaleinae	9.66 ± 0.69	4.61 ± 0.27	3.63	2.34	5.05	7.18	< 0.001
Hemiacridinae	14.76 ± 1.47	9.25 ± 0.89	7.66	5.02	5.51	3.31	< 0.001
Tropidopolinae	11.20 ± 0.25	7.77 ± 0.92	2.76	3.32	3.43	2.85	< 0.001
Oxyinae	17.59 ± 1.41	11.35 ± 0.92	5.47	3.55	6.24	3.19	< 0.001
Coptacridinae	17.0 ± 1.05	11.88 ± 0.88	3.79	3.17	5.12	3.73	< 0.001
Calliptaminae	12.81 ± 1.02	7.83 ± 0.53	3.21	1.77	4.98	4.46	< 0.001
Euryphyminae	15.90 ± 1.29	9.11 ± 0.85	4.46	3.18	6.79	4.52	< 0.001
Eyprepocnemidinae	14.59 ± 1.06	7.01 ± 0.42	4.96	2.02	7.58	6.77	< 0.001
Catantopinae	14.59 ± 0.37	8.63 ± 0.21	4.69	2.97	5.96	14.77	< 0.001
Cyrtacanthacridinae ...	6.98 ± 0.37	4.51 ± 0.20	1.75	1.02	2.47	6.00	< 0.001
**Egnatiinae*	24.68	17.87					
Acridinae	17.18 ± 0.57	10.41 ± 0.35	7.07	4.41	6.77	10.14	< 0.001
**Eremogryllinae*	29.17	17.38					
Truxalinae	20.83 ± 0.68	12.55 ± 0.51	6.29	4.64	7.28	8.55	< 0.001

* Not calculated statistically because too few specimens were available.

dard deviation and standard error (table 15). The males and females were treated separately.

It was found that in every family and subfamily the mean value of the tympanal index was much higher in the males, and sometimes as much as twice that of the females. This indicates that the membrane is always relatively larger in the male than in the female.

The mean tympanal indices of the males and the females were examined statistically, "t" and "P" tests being made. It was found that in every family and subfamily there is a highly significant difference between the sexes in this respect ($P < 0.001$) (table 15).

In *Pamphagidae* the means for the tympanal index: ♂ 9.44, ♀ 4.67, indicating that the membranes are very small in relation to body size. The corresponding figures for *Pyrgomorphidae* are similar but even a little lower. Among the subfamilies of *Acrididae* analysed the highest values for the tympanal index (♂ 20.83, ♀ 12.55) and therefore the largest membranes are in *Truxalinae,* and the smallest are in *Cyrtacanthacridinae* (♂ 6.98, ♀ 4.51). These values are the extremes not only for the family *Acrididae* but also for the whole of *Acridomorpha,* though it may be noted that certain small subfamilies of *Acrididae,* i. e. *Egnatiinae* and *Eremogryllinae,* for which very little material was available for study may have even larger indices than *Truxalinae,* as two males and two females of *Eremogryllinae* gave values of 29.17 and 17.38.

Comparison of tympanal index of "Truxalinae" with that of other families and subfamilies, with special reference to occurence of sound-production mechanisms.

Since the tympanal index is largest in *Truxalinae* and this subfamily also possesses highly developed sound-producing mechanisms, it was decided to compare statistically the index of *Truxalinae* with that of other subfamilies and families, taking into consideration the presence and absence of sound-producing mechanisms. The sexes were treated separately.

The results (table 16) show that the indices of most of the subfamilies of *Acrididae,* and of the families *Pamphagidae* and *Pyrgomorphidae* as such, are highly significantly less in both sexes than those of *Truxalinae,* although the sound-producing mechanisms vary much in form, structure and degree of development, and are sometimes even absent;

in *Pyrgomorphidae* a tympanal organ is usually present but sound-producing mechanisms are quite unknown. In contrast, *Oxyinae* and *Coptacridinae* in both males and females show no significant difference from *Truxalinae* in the tympanal index, yet no stridulatory mechanism is known in either of these two subfamilies.

TABLE 16.

Difference between Truxalinae *and other families and subfamilies in respect of the tympanal index.*

Families and subfamilies	Difference between means		d.f		t		P	
	♂	♀	♂	♀	♂	♀	♂	♀
Truxalinae: Pamphagidae	11.39	7.88	133	131	11.37	11.42	< 0.001	< 0.001
Truxalinae: Pyrgomorphidae ...	12.81	7.93	126	123	9.76	10.23	< 0.001	< 0.001
Truxalinae: Romaleinae	11.17	7.94	112	115	8.90	9.46	< 0.001	< 0.001
Truxalinae: Hemiacridinae	6.07	3.30	111	115	4.14	3.35	< 0.001	< 0.001
Truxalinae: Tropidopolinae	9.63	4.78	96	96	5.21	3.58	< 0.001	> 0.3
Truxalinae: Oxyinae	3.24	1.20	99	98	1.87	0.95	> 0.05	> 0.6
Truxalinae: Coptacridinae	3.83	0.67	97	96	2.13	0.50	> 0.02	< 0.01
Truxalinae: Calliptaminae	8.02	4.72	94	94	3.96	3.33	< 0.001	< 0.01
Truxalinae: Euryphyminae	4.93	3.44	96	97	2.62	2.67	< 0.01	< 0.001
Truxalinae: Eyprepocnemidinae.	6.24	5.54	106	106	4.31	5.57	< 0.001	100·0 >
Truxalinae: Catantopinae	6.24	3.92	248	285	8.82	8.40	< 0.001	< 0.001
Truxalinae: Cyrtacanthacridinae.	13.85	8.04	106	105	10.19	8.04	< 0.001	< 0.001
Truxalinae: Acridinae	3.65	2.14	238	240	3.97	3.52	< 0.001	< 0.001

TABLE 17.

The mean, standard deviation, standard error and the difference between the means of the tympanal indexes of the sexes of the wing groups in the families and subfamilies.

Family or subfamily	Mean and Standard Error		Standard Deviation		Difference between means ♂ - ♀	d. f.	t	P
	♂	♀	♂	♀				
Pamphagidae:								
Macropterous	8.98 ± 0.53	5.54 ± 0.36	2.64	1.25	3.44	35	4.27	< 0.001
Micropterous	10.05 ± 0.59	4.61 ± 0.26	2.56	1.21	5.44	38	8.74	< 0.001
Pyrgomorphidae:								
Macropterous	8.62 ± 1.04	4.60 ± 0.57	4.79	2.40	4.02	37	3.22	< 0.01
Micropterous	8.58 ± 0.68	5.10 ± 0.49	2.72	2.09	3.48	32	4.20	< 0.001
Acrididae:								
Macropterous	15.86 ± 0.31	9.70 ± 0.21	6.24	4.33	6.16	818	16.49	< 0.001
Brachypterous	16.16 ± 0.88	8.61 ± 0.43	5.45	3.36	7.55	96	8.49	< 0.001
Micropterous	17.55 ± 0.63	9.62 ± 0.33	6.66	3.74	7.93	240	11.61	< 0.001
Apterous	11.48 ± 1.54	6.69 ± 0.95	5.05	3.14	4.80	20	2.66	< 0.001
Romaleinae:								
Macropterous	8.36 ± 2.23	4.32 ± 0.41	3.00	1.77	4.05	34	4.96	< 0.001
Micropterous	10.35 ± 1.61	5.11 ± 0.41	4.67	1.07	5.25	12	3.15	< 0.01
Hemiacridinae:								
Macropterous	13.00 ± 1.04	8.92 ± 0.90	4.76	3.92	4.08	38	2.94	< 0.01
Tropidopolinae:								
Macropterous	10.91 ± 1.15	6.60 ± 0.86	3.25	2.58	4.31	15	3.04	< 0.01
Oxyinae:								
Micropterous	18.08 ± 1.50	11.32 ± 1.27	4.51	4.02	6.76	17	3.46	< 0.01
Coptacridinae:								
Macropterous	16.22 ± 1.05	9.88 ± 0.93	3.17	2.78	6.34	16	4.51	< 0.001
Calliptaminae:								
Macropterous	13.14 ±1.05	8.54 ± 0.60	2.78	1.58	4.60	11	3.95	< 0.01
Euryphyminae:								
Macropterous	16.45 ± 1.48	9.47 ± 1.14	4.66	3.61	6.98	18	3.74	< 0.01
Eyprepocnemidinae:								
Macropterous	12.69 ± 1.04	6.36 ± 0.47	4.04	1.81	6.33	28	5.54	< 0.001
Micropterous	18.65 ± 1.67	8.76 ± 0.50	4.44	1.29	9.90	12	5.67	< 0.001
Catantopinae:								
Macropterous	13.61 ± 0.38	8.43 ± 0.28	3.50	2.87	5.17	185	11.12	< 0.001
Brachypterous	14.63 ± 1.36	8.95 ± 0.64	4.92	2.99	5.68	33	4.27	< 0.001
Micropterous	16.44 ± 0.70	9.07 ± 0.38	5.35	3.10	7.37	122	9.52	< 0.001
Apterous	12.04 ± 1.58	7.13 ± 0.93	5.01	2.93	4.91	18	2.67	< 0.02
Acridinae:								
Macropterous	16.62 ± 0.58	10.50 ± 0.39	6.77	4 53	6.12	272	8.78	< 0.001
Micropterous	23.59 ± 1.92	11.34 ± 0.83	7.18	3.12	12.25	26	5.85	< 0.001
Truxalinae:								
Macropterous	20.71 ± 0.77	12.88 ± 0.60	6.45	4.86	6.98	18	3.74	< 0.01
Micropterous	20.24 ±1.32	11.50 ± 0.78	4.77	2.72	8.74	23	5.56	< 0.001

In general, therefore, one must conclude, rather surprisingly, that there is no relationship between the occurrence of tympanal organs and of known sound-producing mechanisms at family or subfamily level.

Correlation between tympanal index and length of tegmina.

It was previously thought that the length of the tegmen and the size of the tympanal membrane were correlated i. e. that reduction in wing size is followed by reduction of the tympanal membrane. This problem was therefore investigated.

The tegmina can be divided into four groups: macropterous, i. e. fully winged specimens with tegmina reaching or exceeding the end of the abdomen and overlapping dorsally; brachypterous, i. e. with tegmina shorter than the abdomen but overlapping dorsally; micropterous, i. e. with short tegmina not overlapping dorsally; and apterous, i. e. with no trace of tegmina or wings.

The mean tympanal index was calculated for each wing group in each main family and subfamily. The males and females were treated separately.

In every wing group in all families and subfamilies studied the difference between the means of the tympanal indices of the males and females was highly significant (table 17). The means also showed that the males in every wing group have much larger membranes in relation to body size than the females.

The families investigated were *Pamphagidae, Pyrgomorphidae* and *Acrididae,* and the subfamilies were those of *Acrididae.* The standard deviation and standard error for each wing group were calculated for males and females (table 17). It was found that in every case the males have a larger standard deviation than the females.

For *Pamphagidae* the means of the micropterous group are ♂ 10.05, ♀ 4.61; and the means of the macropterous group are ♂ 8.98, ♀ 5.54. This indicates that the male membranes are larger in the micropterous group, and the female membranes slightly larger in the macropterous group.

The *Pyrgomorphidae* gave opposite results, but this family (see fig. 13, *b*) is a heterogeneous complex. The means of the macropterous group are ♂ 8.62, ♀ 4.60; and those of the micropterous group are ♂ 8.58, ♀ 5.10.

TABLE 18.

Difference between means of male and female tympanal indices of wing groups in some families and subfamilies.

Family or subfamily	Difference between means		d. f.		t		P	
	♂	♀	♂	♀	♂	♀	♂	♀
Pamphagidae:								
Micropterous — Macropterous	1.07	0.84	42	31	1.35	1.89	> 0.10	> 0.05
Pyrgomorphidae:								
Macropterous — Micropterous	0.04	0.50	35	34	0.03	0.66	> 0.9	> 0.5
Acrididae:								
Romaleinae								
Micropterous — Macropterous	1.99	0.80	23	23	1.33	1.12	> 0.1	> 0.20
Eyprepocnemidinae:								
Micropterous — Macropterous	5.97	1.39	20	20	3.13	3.13	< 0.01	< 0.01
Catantopinae:								
Micropterous — Brachypterous	1.81	0.12	69	86	1.12	0.17	> 0.2	> 0.8
Micropterous — Macropterous	2.83	0.64	139	168	3.80	1.37	< 0.001	> 0.1
Micropterous . ... Apterous	4.4	1.94	66	74	2.43	1.86	< 0.02	> 0.05
Brachypterous — Macropterous	1.02	0.51	94	124	0.92	0.76	> 0.3	> 0.4
Brachypterous — Apterous	2.59	1.82	21	30	1.24	1.61	> 0.2	> 0.1
Macropterous — Apterous	1.57	1.30	91	112	1.28	1.37	> 0.2	> 0.1
Acridinae:								
Micropterous — Macropterous	6.97	0.84	150	148	3.65	0.68	< 0.001	> 0.4
Truxalinae:								
Macropterous — Brachypterous	0.47	1.38	81	75	0.25	0.95	> 0.8	> 0.3

The *Acrididae* proved similar to *Pamphagidae* in this respect, particularly in the males. The male tympanal index was higher in the micropterous than in the macropterous group in the family as a whole and also in all those subfamilies in which these two groups were represented in the material studied. Thus there are indications that the tympanal membrane of the male is larger, relative to body size, in the micropterous than in macropterous species of *Acrididae,* and a similar tendency is apparent in the females at subfamily level (table 17).

The tympanal index is conspicuously lower for apterous *Acrididae* (and for *Catantopinae,* the only subfamily suitably analysed) than for any other wing group.

However, further analysis (table 18) shows that several of the differences between wing groups on which these general conclusions are based are non-significant, but those which stand out as significant are as follows for the males of *Catantopinae,* micropterous minus macropterous and micropterous minus apterous; for the males of *Acridinae,* micropterous minus macropterous; and for both the males and the females of *Eyprepocnemidinae,* micropterous minus macropterous.

KEY TO FAMILIES BASED ON THE TYMPANAL ORGAN (WHEN PRESENT).

1 (2) Sclerotic cavity absent. Sclerotic structure small (rarely absent), consisting of one thin elongate nerve-like body (fig. 2, *d*), extending from the lower anterior corner of the membrane towards the centre of it ... ... **Pyrgomorphidae.**

2 (1) Sclerotic cavity present (except when the tympanal organ is poorly developed). Sclerotic structure large, centrally situated and not extending from the lower anterior corner of the membrane (fig. 2, *a, b, c, e, f, g*).

3 (4) The sclerotic structure does not possess a pyriform vesicle or fusiform body (fig. 2, *b, c*) ... ... **Pamphagidae, Charilaidae.**

4 (3) The sclerotic structure possesses a pyriform vesicle and fusiform body (fig. 2, *a, e, f, g*).

5 (6) The sclerotic structure possesses one main sclerotic body (fig. 2, *g*). The first abdominal spiracle is slit-like. **Pauliniidae.**

6 (5) The sclerotic structure possesses a folded body and styliform body (fig. 2, *a, e, f*). The first abdominal spiracle is not slit-like ... ... **Acrididae, Ommexechidae.**

Discussion and conclusions.

Examination of both males and females from 915 genera of the whole world fauna of *Acridomorpha* showed that the families *Eumastacidae, Proscopiidae, Tanaoceridae, Pneumoridae, Xyronotidae, Trigonopterygidae, Lathiceridae, Lentulidae* and the subfamily *Lithidiinae* do not possess tympanal organs, but the families *Charilaidae, Pamphagidae, Pyrgomorphidae, Ommexechidae, Pauliniidae* and sixteen subfamilies of *Acrididae* usually possess them.

The general external morphology of the tympanal organ shows that it may be useful as a taxonomic character for families or groups of families. Some subfamilies have features of the tympanal organ distinguishing them entirely from the rest; in other subfamilies the characters vary greatly, but sometimes they may serve to distinguish genera.

Uvarov (1966) in his book on "Grasshoppers and Locusts" states that there is a tendency for degeneration of the tympanal organ to be related to the loss of ability to fly and suggests that the tympanal organ may be connected with echolocation. However, from the present study it was concluded that although certain external features, notably the shell covering, subtympanal lobe and degree of depth of the membrane, are reduced with the reduction of wing size, the relative size of the membrane is, in general, larger in micropterous species, smaller in brachypterous species and smaller still in macropterous species (table 17, especially *Catantopinae).*

The subtympanal lobe when present is larger in the macropterous groups, smaller in the brachypterous and usually absent or reduced to a mere ridge in the micropterous groups. There is a corresponding reduction in the size of the dorsal shell covering, but it is usually not so reduced as the subtympanal lobe. There are nearly always traces of the dorsal shell covering in micropterous specimens, in which the membrane seems to be generally protected by the shortened tegmina. In brachypterous and micropterous specimens the membrane is less depressed beneath the body wall than in macropterous specimens, but at the same time its diameter becomes larger. These tendencies may help to indicate whether a specimen is correctly placed taxonomically.

When the membrane is characteristically present and transparent in a family, in apterous specimens of that family it is frequently small, sclerotized or vestigial. The apterous specimens have no shell cover-

ing or subtympanal lobe, and the membrane is completely level with the cuticle. Moreover, the sclerotic supports of the sense organ virtually disappear and the membrane is greatly reduced in size until only a very small sclerotized vestige is left.

The principal conclusions from this investigation can be summarised as follows:

1. The absolute membrane size increases with increase of body size in both sexes but the rate of increase differs among the families and subfamilies.
2. The tympanal index indicates that the average size of the membrane, relative to the body size, is much larger in the male than in the female.
3. In *Acridoidea* the smallest membranes, relative to body size, are found in *Cyrtacanthacridinae* and the largest in *Truxalinae.*
4. *Pamphagidae, Pyrgomorphidae* and all subfamilies of *Acrididae* except *Oxyinae* and *Coptacridinae* have highly significantly smaller membranes than *Truxalinae;* in both sexes.
5. In every wing group (macropterous, brachypterous, micropterous and apterous) in all families and subfamilies the membrane is highly significantly larger in the male than in the female.
6. In *Pamphagidae* the membrane in the micropterous groups is larger than that in the male macropterous groups, and the reverse applies in the females but with low significance.
7. In *Catantopinae,* the largest subfamily of *Acrididae,* there is a general tendency for the largest membranes to be found in the micropterous groups, smaller ones in the brachypterous groups, still smaller ones in the macropterous groups and the smallest in the apterous groups. This applies in both sexes.
8. In the males of *Catantopinae, Acridinae* and *Eyprepocnemidinae* the membrane is hightly significantly larger in the micropterous group than in the macropterous group. In the males of *Catantopinae* the membrane is highly significantly larger in the micropterous group than in the apterous group.
9. In the females of *Catantopinae, Acridinae, Truxalinae, Eyprepocnemidinae* and *Romaleinae* the differences in membrane size between the various wing groups are highly significant in *Eyprepocnemidinae* only.
10. *Romaleinae* is the only subfamily in which the membrane of the

micropterous group shows no significant difference in size to the membrane of the macropterous group, in either sex.

11. In *Truxalinae* no significant difference was found between the size of the membranes of the macropterous and brachypterous groups.

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